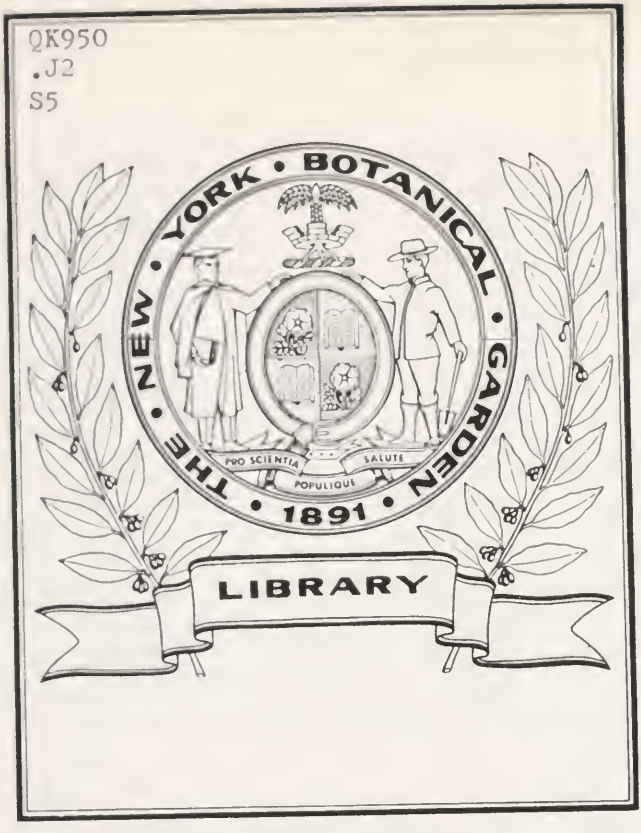
A MONTANE RAIN-FOREST

A CONTRIBUTION TO THE PHYSIOLOGICAL PLANT GEOGRAPHY OF JAMAICA

By FORREST SHREVE

QK950
.J2
S5


THE • NEW • YORK • BOTANICAL • GARDEN
PRO SCIENTIA ... SALUTE
POPULIQUE
1891
LIBRARY

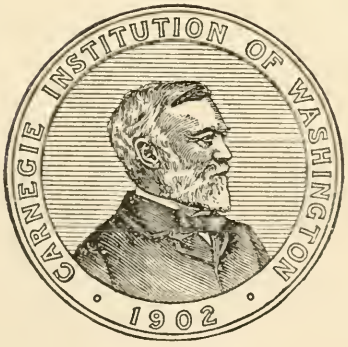
Floor of a Windward Ravine near Morce's Gap at 5,000 feet altitude. In the center the tree-fern *Cyathea pubescens*, in the foreground *Diplazium celtidifolium* and *Diplazium altissimum*.

A MONTANE RAIN-FOREST

A CONTRIBUTION TO THE PHYSIOLOGICAL PLANT GEOGRAPHY OF JAMAICA

BY

FORREST SHREVE



WASHINGTON, D. C.
PUBLISHED BY THE CARNEGIE INSTITUTION OF WASHINGTON
1914

.S5

CARNEGIE INSTITUTION OF WASHINGTON
PUBLICATION NO. 199

Copies of this Book
were first issued
SEP 12 1914

PRESS OF GIBSON BROTHERS, INC.
WASHINGTON, D. C.

CONTENTS.

PAGE.

Introduction 5
The Physical Features of the Rain-forest Region 7
General Climatology of the Rain-forest Region 10
Air Temperature 10
Nocturnal Terrestrial Radiation 11
Soil Temperature 12
Humidity and Fog 13
Rainfall 13
Sunshine and Cloudiness 16
Wind 17
The Flora of the Rain-forest 18
The Vegetation of the Rain-forest 22
Ecological Characteristics of the Rain-forest 22
Habitat Distinctions in the Rain-forest 26
Windward Ravines 28
Windward Slopes 31
Leeward Ravines 32
Leeward Slopes 33
The Ridges 35
The Peaks 37
Epiphytes 38
The Relation of Physical Conditions to Habitat Distinctions in the Rain-forest 41
Humidity 44
Evaporation 46
Air Temperature 48
Soil Temperature 49
Seasonal Behavior of the Rain-forest Vegetation 51
Rate of Growth in Rain-forest Plants 55
Transpiration Behavior of Rain-forest Plants 59
Methods and Material 59
Daily March of Transpiration 62
Individual Variability of Transpiration Rate 72
Concurrent Rates of Transpiration in Different Species 73
Relative Transpiration 76
Comparison of Relative Transpiration Rates in Rain-forest and Desert Plants 82
Relative Amounts of Stomatal and Cuticular Transpiration 87
Stomatal Behavior 91
Influence of Darkness on Transpiration 99
Influence of High Humidity on Transpiration 102
General Conclusions 106

INTRODUCTION.

The vegetation of Jamaica is of particular interest, both by reason of the wealth of the flora of which it is made up and because of the diversity which is given it by the varied geological, topographic, and climatic conditions which exist within the limits of so small an island. Jamaica lies in the center of the Caribbean Sea in 18° N. latitude, is about 150 miles long, and from 25 to 50 miles wide. Its most salient physical feature is the central mountainous axis, the eastern end of which is lofty and of relatively recent geologic age, while the western two-thirds are lower and older; the recent formations being mostly shales, conglomerates, and tuffs, the older limestone. The mountainous interior is bordered on the north by a very narrow coastal plain, on the south by a plain which is narrow opposite the loftier mountain mass, but wide in the southwestern parishes of the island. The higher elevations of the eastern end constitute the Blue Mountain Range, which attains to an altitude of 7,428 feet (2,264 meters). Not only do the Blue Mountains present conditions of temperature that result in their own vegetation being distinct from that of the lowlands, but they moreover serve as a barrier to the trade winds, and thereby give differences of rainfall and humidity on their north and south sides which are of importance in determining the character of the lowland vegetation. The greatest rainfall in the island is registered at high elevations on the northern slopes of the Blue Mountains, while the least occurs at the coast to the south of them. The lower and older portion of the mountainous axis, which reaches its highest points in Mount Diablo, Bull Head, Dolphin Head, and the Santa Cruz Mountains, is much less diversified than the Blue Mountains in both temperature and rainfall conditions, and strikingly dissimilar to any part of them in its vegetation. South of the older mountainous region are broad savannas, with morasses along the larger streams and deserts on certain parts of the coast.

There is perhaps no tropical area of its size in the world that has received more painstaking and prolonged attention at the hands of collectors and taxonomists than has Jamaica. From the reconnaissances of Sir Hans Sloane, the first botanical visitor to the island, in 1687, down to the methodical campaign which has been made during the last twenty years against all the less-known parts of the island, there has been a steady stream of additions to the flora, in which over forty botanists have taken a hand. During these two centuries of floristic activity there has been, however, but a single visitor interested in the vegetation of the island in its physiognomic and physiological aspects, the Danish botanist Örsted. He visited the island in 1846 and published a paper entitled "Skildring af Naturen paa Jamaica," which is a brief description of the vegetation, strikingly modern in its manner and as accurate as his brief visit of six weeks would permit.

In spite of the fact that Jamaica was the first portion of the Western Hemisphere to reach a high and valuable agricultural productivity, there is still much of it that has been left untouched by the Spanish and English occupants of the island, either because of its inaccessibility or of the worthlessness of both the land and its natural covering. These are the very localities which are most interesting to the botanist, because of their being the places where the factors controlling plant occurrence are operating in the most extreme degree. The higher Blue Mountains, the limestone mountains of the central region, the exsected limestone region known as the "Cockpit Country," the coastal deserts, the morasses and the mangrove swamps, as well as the algal formations, are all calculated to interest the student of vegetation in the highest degree.

During three visits to Jamaica I have had opportunities to see something of all the above-mentioned formations, excepting the larger morasses and the heart of the Cockpit Country, and have been able to spend a total of eleven months in the Blue Mountain Region at Cinchona, the Tropical Station of the New York Botanical Garden. Cinchona is situated on a spur projecting south from the Main Ridge of the Blue Mountains, at an elevation of 5,000 feet (1,525 meters). I first visited it in April 1903, in company with Dr. D. S. Johnson; for the second time from October 1905 to May 1906, while holding the Adam T. Bruce Fellowship in the Johns Hopkins University; and for the third time from July to November 1909, while absent from the Desert Laboratory.

My last two visits to the Blue Mountains have been given to gaining an acquaintance with the common and characteristic components of its flora, to a study of the distribution of the vegetation within the mountain region, and a study of the differences in physical conditions which underlie the distinctness of the several habitats, as well as to an investigation of some of the physiological activities of plants confined to the rain-forest region. In the following pages I am presenting my results on the general physiological plant geography of the Rain-Forest Region, as well as my investigations on transpiration and growth in typical rain-forest forms.

I wish here to thank Dr. N. L. Britton, Director of the New York Botanical Garden, for the facilities and equipment which were put at my disposal in Jamaica by the Garden. To Dr. D. T. MacDougal and Dr. D. S. Johnson I wish to express my thanks for their personal interest in my work during both visits. I wish also to thank the Hon. William Fawcett, former Director of Public Gardens and Plantations of Jamaica, for many substantial kindnesses shown me during my second visit in the island; and to William Harris, esq., Superintendent of Public Gardens and Plantations, my thanks are due for assistance in taxonomic matters as well as for many services essential to the prosecution of my work.

THE PHYSICAL FEATURES OF THE RAIN-FOREST REGION.

The Blue Mountains lie in a WNW.-ESE. position, being midway between the north and south coasts and parallel with them. The range extends from Silver Hill in the west to Cunhacunha Pass in the east, a distance of 22 miles. The first considerable elevation in the western end is John Crow Peak (6,000 feet, 1,830 meters), which is separated by Morce's Gap (4,934 feet, 1,505 meters) from a comparatively level ridge which runs from an unnamed elevation (about 5,800 feet, 1,770 meters), through New Haven Gap (5,600 feet, 1,705 meters), Sir John Peter Grant Peak (about 6,200 feet, 1,890 meters), and Mossman's Peak (about 6,900 feet, 2,105 meters) to Portland Gap (5,550 feet, 1,695 meters). To the east of Portland Gap the ridge rises abruptly to its summit in Blue Mountain Peak (7,428 feet, 2,265 meters). From its sister peak, the Sugar Loaf, the range descends gradually eastward to Cunhacunha Pass. To the north and south of the Main Ridge, lesser ridges diverge toward the sea, dropping in altitude with a rapidity which may be judged from the fact that the coast is in no place more than 13 miles from the Main Ridge. To the east of Cunhacunha Pass lies the Blake, or John Crow, range, running parallel to the eastern coast and having an average elevation of about 2,100 feet (640 meters). Again, to the south of the Blue Mountains lies a range known in part as the Port Royal Mountains, which have their greatest elevation in Catherine's Peak (5,036 feet, 1,535 meters) and rise to nearly that height at other places.

In the following pages I have confined my treatment to the Blue Mountains proper above an elevation of 4,500 feet (1,372 meters). On descending below this altitude the flora of the mountains is rapidly left behind and the climate is found to be not only warmer but drier and less foggy, at the same time that the virgin forest begins to give place to vegetable and coffee fields. The accompanying map (plate 1) has been drawn from Liddell's survey (published by Stanford) and the contours have been sketched in from eight known elevations. The contours have been used only for the sake of giving a graphic approximation of the extent and configuration of the area under consideration. The roads and trails indicated are the only ones in the area, and the character of the topography and vegetation makes it laborious to penetrate very far beyond them. Although I have made visits to Portland Gap and Blue Mountain Peak, the region is best known to me in its western part between John Crow and Sir John Peaks and between Cinchona and Vinegar Hill, and it is within this part that all of my instrumentation has been carried on.

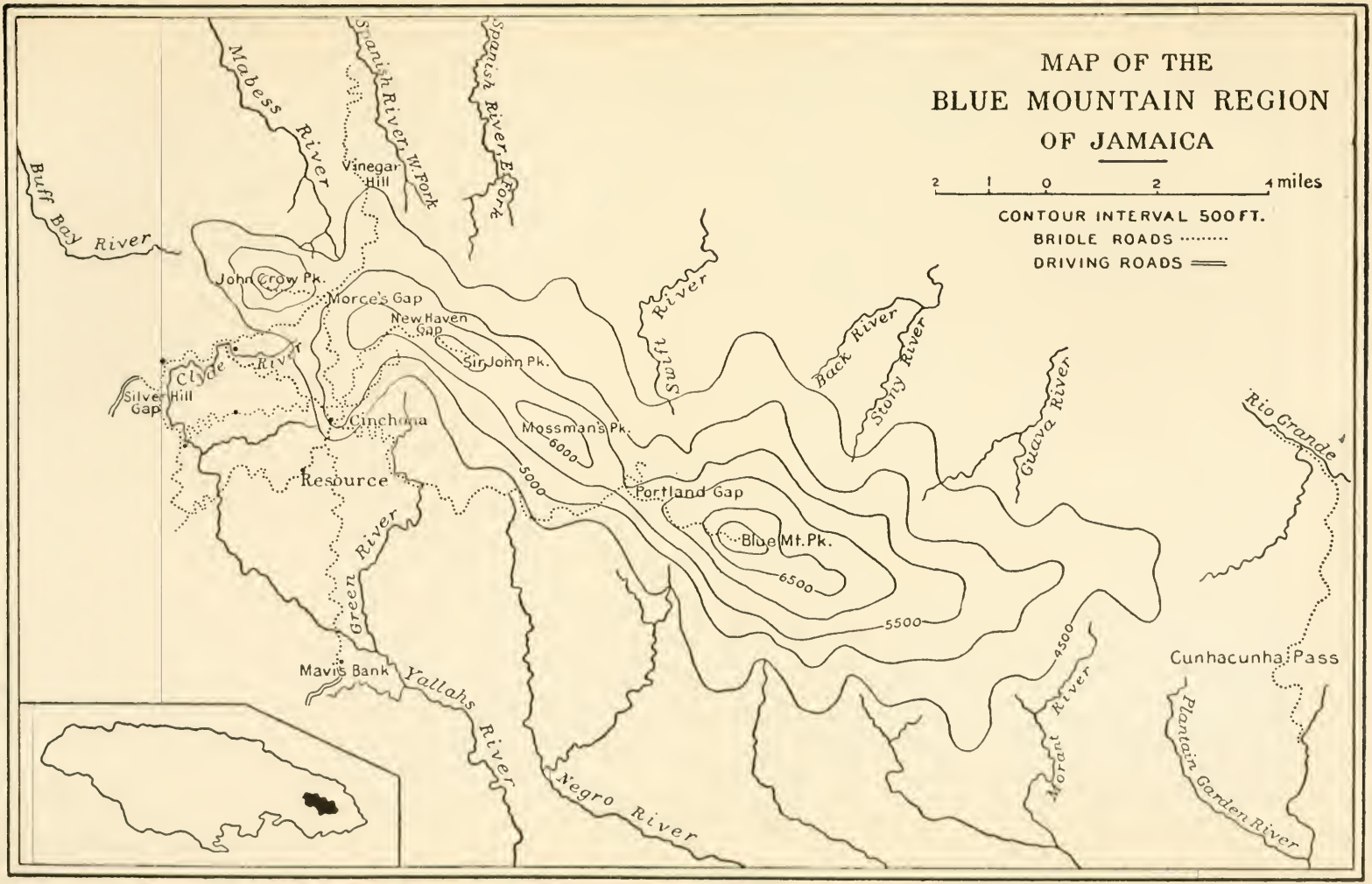
There are no traces of recent volcanic activity in the Jamaican mountains and they present to-day the rounded summits and closely set valleys of a typical erosion topography. The underlying rock is mainly readily weathered shale. At the summit of John Crow Peak and at a few localities in the Clyde and Green River valleys there are outcroppings of limestone. In spite of the copious rainfall there are no constant streams above 4,500 feet, but at a very few hundred feet below that elevation the water table emerges to feed numerous swift streams. Owing to the nature of the topography, there are no lakes or ponds, although there are a few depressions on the summit of the Main Ridge itself, which are developed as sphagnum bogs.

The longer lateral ridges which form the divides between large drainage areas are comparatively gentle in slope (14° to 25°). Those ridges which separate smaller drainage areas are steeper (25° to 35°). The flanks of these ridges are, of course, steeper still (35° to 45°) and in narrow ravines the sides are frequently as steep as 65°. Such precipitous slopes, in the absence of resistant rock, are a resultant between the erosive action of the abundant rainfall and run-off and the retaining action of the vegetation. The former of these forces frequently overcomes the latter and landslips take place which devastate the vegetation and leave paths which remain unstable and bare for a long time.

The deepest of the soils is a yellow clay which occurs on ridges and gentle slopes in a few localities in the vicinity of the limestone outcrops, and sometimes attains to a depth of 8 feet. With this exception the soils are shallow and filled with coarse rock fragments. Their humus content is high, but the rapidity of erosion prevents its accumulation.

The climate of the Blue Mountains is that of all mountainous regions in tropical islands. The temperatures are extremely constant and low as compared with those in the lowlands, although very rarely so low as to make frost possible, and the rainfall is abundant at all seasons. The Blue Mountain Region is, therefore, a tropical montane region, in the terms of Schimper, lying above the hot lowlands and not attaining to a sufficient altitude for alpine influences to come into full play. The dominant vegetation is, in accordance with the climate, the evergreen broad-leaved forest, which is here of a type strongly temperate in its floristic make-up and in its vegetative characteristics.

The economic value of the forests and lands of the Blue Mountain Region is low, as has been hinted in the Introduction. A very small amount of timber is taken out of the forests from time to time to supply the framework for bamboo houses in the neighboring settlements, but the bulk of it stands to-day untouched. Although there are several valuable woods among the mountain trees, notably that of the *Podocarpus*, natural obstacles make the forests commercially worthless and they are held as Crown Land for the sake of their value as a cover and


MAP OF THE
BLUE MOUNTAIN REGION
OF JAMAICA
2 1 0 2 4 miles
CONTOUR INTERVAL 500 FT.
BRIDLE ROADS
DRIVING ROADS
Mabess River
Spanish River W. Fork
Spanish River E. Fork
Vinegar Hill
Buff Bay River
John Crow Pk.
Morce's Gap
New Haven Gap
Sir John Pk.
Swift River
Back River
Stony River
Guava River
Rio Grande
Clyde River
Silver Hill Gap
Cinchona
Mossman's Pk.
6000
5000
Resource
Portland Gap
Blue Mt. Pk.
6500
5500
4500
Green River
Mavis Bank
Yallahs River
Negro River
Morant River
Plantain Garden River
Cunhacunha Pass

a source of water supply. At present the only extensive agricultural operations in the Blue Mountains are the planting of Arabian coffee, which grows successfully on the southern slopes up to 4,500 and 5,000 feet. Above this altitude, and on the northern slopes, it grows well but does not bloom and produce berries abundantly enough to be profitable. Assam tea grows well at from 4,800 to 5,500 feet, but has never been planted extensively. For a number of years the cultivation of Cinchona, or Peruvian bark, was carried on very successfully at from 4,500 to 5,900 feet, and there are now no natural obstacles to its production, indeed *Cinchona officinalis* has become naturalized in the vicinity of some of the old fields. On the southern slopes, from 5,000 feet downward, at least one-third of the land is out of cultivation and covered with a scrub of xerophilous bushes, known locally as "ruinate." Indications point to the reforestation of the ruinate as being a very slow process, as some of it which has not been touched for twenty-four years is far from having the beginnings of a stand of forest trees.

The precipitate slopes on which coffee is grown are very liable to landslips. During the heavy rains of November 1909, hundreds of acres of coffee were destroyed in this way, and the areas they occupied must remain unstable and bare for many years. The landslips that were conspicuous in April 1903, when I first visited the Blue Mountains, were still bare of vegetation when I last saw them in November 1909. The heavy rains of that month did not cause an enlargement of the old landslips, but created new ones, some of which reached up into the virgin forest, where as a rule only small landslips occur. In the vicinity of Cinchona I have seen areas of ruinate, in which there were numerous landslips, that I was told, on creditable authority, were abandoned as coffee fields over fifty years ago on account of the excessive erosion. The indications are that the precipitate topography of the coffee-growing region will ultimately lead to its abandonment for all uses except the growing of vegetables, which is now carried on extensively by the negro peasants. The yam, the coca (*Colocasia antiquorum*), the sweet potato, the turnip, the parsnip, and a small onion (*Allium fistulosum*) are all successfully grown in small patches protected from erosion by abatis of twigs and sticks.

GENERAL CLIMATOLOGY OF THE RAIN-FOREST REGION.

The following data on the climatology of the Montane Rain-Forest region are based on the records kept at Cinchona, at New Haven Gap, and at Blue Mountain Peak by the Jamaican Department of Public Gardens and Plantations, which are the only records ever kept in the higher Blue Mountains. The observations made at these localities were published currently in the Bulletin of the Botanical Department of Jamaica and in the Jamaica Gazette, but have never been subjected to a systematic analysis. I have secured data for several features (such as the number of rainy days) by an inspection of the manuscript records of the Department.

Using these data as a basis I have endeavored to determine to what extent the physical conditions in certain typical plant habitats depart from the climatic conditions of the region as a whole, and in just what respects the several habitats differ from each other. I obtained records with an air thermograph, a hygrograph, a soil thermograph of the Hallock type, and atmometers of the type devised by Livingston. These results will be presented in the chapter on the relation of physical conditions to habitat distinctions (see p. 41).

AIR TEMPERATURE.

The record of air temperatures for Cinchona consists of daily readings of the maximum and minimum and of the current temperatures at 7 a. m. and 3 p. m. In view of the constancy of temperature conditions a digest of these records for fifteen years (1891–1905 inclusive) has seemed sufficient to give an accurate set of means and ranges. Owing to the unfortunate custom of making a reading at 3 p. m., it has been necessary to determine the daily mean by taking half the sum of the minimum and the 3 p. m. temperatures.[1] In table 1 are exhibited the principal elements of the climate as respects temperature.

At New Haven Gap a set of observations of the monthly absolute maximum and minimum was taken during the years 1882 to 1893 at a cleared spot in the summit of the Gap at 5,600 feet (1,705 meters) elevation. During the twelve years of these observations there are 26 monthly readings missing. A set of observations of absolute monthly maximum and minimum was also taken at Blue Mountain Peak during the years 1890 to 1900, the instruments being exposed upon the cleared summit of the peak at an elevation of 7,428 feet (2,264 meters). From this record two months are missing. For the sake of comparison I have found by inspection the absolute monthly maximum and minimum for Cinchona for the years 1891 to 1900, and table 2 exhibits the means of these data for the three localities for the years mentioned:

The absolute maximum for Blue Mountain Peak is 76° in September 1891, the absolute minimum 33.3° in February 1893; the absolute maxi-

[1]Hann, Handbook of Climatology, Transl. by Ward, p. 8. New York, 1903.

A. Looking east along the leeward slopes of Mossman's Peak and Blue Mountain Peak from an altitude of 5,500 feet. The white areas are coffee fields.

B. Looking southwest from the vicinity of Cinchona into the valley of Clyde River. Slopes of John Crow Peak are on the right.

mum for New Haven Gap is 83° in July 1889, and the absolute minimum 40.5° in January, February, and April 1888. Not only are the averages of the monthly absolute maxima and minima unsatisfactory data from which to determine the temperature conditions for a locality, but the fact that these figures do not cover the same years in the case of New Haven Gap as for the other localities invalidates too close comparison of them. The more exposed position of New Haven Gap on the Main Ridge, as compared with Cinchona, will account for its greater range of temperature, the difference in altitude being but 600 feet. Between New Haven Gap and Blue Mountain Peak there is a greater difference in altitude (1,828 feet, 555 meters); while the temperatures range lower at the latter place the annual and daily ranges are probably nearly the same.

TABLE 1.—*Monthly mean temperature data for Cinchona, 1891 to 1905.*

	Jan.	Feb.	Mar.	Apr.	May.	June.	July.	Aug.	Sept.	Oct.	Nov.	Dec.
Monthly absolute maximum.	73	75	72	77	74	76	79	80	75	74	75	72
Monthly mean maximum...	66.9	67.0	67.0	67.5	68.3	69.9	71.9	71.8	70.6	68.7	68.3	66
Monthly mean.....	58.8	58.3	58.6	59.3	61.0	62.3	63.1	63.6	62.9	61.8	61.0	59
Monthly mean minimum...	53.4	53.7	53.9	55.3	57.3	58.3	58.8	58.8	59.3	58.7	57.3	55
Monthly absolute minimum.	46	46	47	47	50	50	52	54	51	54	51	47
Daily range.....	13.5	13.3	13.1	12.2	11.0	11.6	13.1	13.0	11.3	10.0	11.0	11

Annual mean temperature.....	60.8°	(16.0° C.).
Annual mean range.....	5.3°	(2.9° C.).
Average daily range.....	12.0°	(6.6° C.).

TABLE 2.—*Monthly absolute maximum and minimum temperatures at Cinchona, New Haven Gap, and Blue Mountain Peak.*

	Jan.	Feb.	Mar.	Apr.	May.	June.	July.	Aug.	Sept.	Oct.	Nov.	Dec.
Maxima:												
Cinchona.....	70.3	71.4	70.9	72.3	72.5	74.0	75.4	76.0	74.2	72.8	72.2	70.5
New Haven Gap.....	69.1	65.7	72.2	73.7	75.2	76.3	76.0	74.6	77.5	74.7	72.7	70.6
Blue Mountain Peak....	69.0	67.0	69.1	70.0	68.5	70.0	68.5	70.4	71.3	70.2	68.2	68.8
Minima:												
Cinchona.....	49.5	49.6	49.3	50.9	53.3	54.9	55.4	55.8	56.3	55.2	53.3	50.3
New Haven Gap.....	47.4	46.0	46.8	48.2	50.3	52.9	54.3	55.3	55.0	54.6	51.1	47.4
Blue Mountain Peak....	38.3	40.9	42.7	40.8	44.6	45.6	46.1	45.5	45.7	45.9	42.2	39.3

NOCTURNAL TERRESTRIAL RADIATION.

Several observations were made on nocturnal terrestrial radiation, with a view to determining what are the probable temperatures at the surface of the ground at the time of some of the low minimum winter temperatures. Ordinary thermometers were laid on a grass sod or lightly covered with earth on a flower bed; another thermometer was placed 3 feet from the ground and compared with a standard thermometer in a Stevenson screen.

In 1906 the night of January 12 was clear and still; that of February 28 was clear with a high wind; that of January 13 was clouded and still. The readings were as follows:

TABLE 3.

Date.	Time.	Air temperature.	On grass.	On earth.	Difference between air and earth.	Difference between air and grass.
January 12..	9h 00m p.m.	54	50.3	49.6	4.4	...
	10h 00m p.m.	55	50.3	48.3	6.7	...
	11h 00m p.m.	54	47.6	46.7	7.3	...
January 13..	9h 45m pm.	59	55.4	....	....	3.6
	10h 00m p.m.	56	55.4	....	....	.6
February 28.	8h 30m p.m.	59	....	48.5	10.5	...
	10h 30m p.m.	55	....	49.6	5.4	...

These observations, taken on the open lawn at Cinchona, show that the temperatures to which herbaceous vegetation in open situations may be subjected are as much as 10.5° lower than the recorded air temperatures on clear nights when active radiation is possible. The fact that radiation takes place most actively during the early hours of the night, while the minimum temperature is always reached just before daybreak, makes it necessary to derive the lowest temperatures due to radiation by subtracting 10° or thereabouts from a temperature higher than the lowest minimum as shown by the records of monthly extremes. This would still indicate the possibility of occasional frost at Blue Mountain Peak, but probably no frost has ever taken place at altitudes lower than 6,500 feet (1,980 meters). The open character of the vegetation on the higher peaks and ridges, to be presently described, would make possible an amount of radiation sufficient to give a depression as great as that observed at Cinchona.

SOIL TEMPERATURE.

Readings of the temperature of the soil at a depth of 6 feet were made at Cinchona for five years, the apparatus being an ordinary driven thermometer in metal casing. The instrument stood in ground covered by a sod and was read twice daily, at 7 a. m. and 3 p. m. The mean of these readings, when they were not the same, is taken as the daily mean and in table 4 are exhibited the monthly means for the years 1892 to 1896, inclusive.

TABLE 4.

Month.	Mean temp.	Month.	Mean temp.
January.....	61.4	July.....	62.2
February.....	60.8	August.....	62.5
March.....	60.5	September.....	63.3
April.....	60.4	October.....	62.9
May.....	60.2	November.....	62.6
June.....	60.8	December.....	61.9

Annual mean..... 61.6° (16.4° C.)
Annual mean range..... 2.9° (1.5° C.)

It may be noted that the annual minimum falls in May, three months after the minimum for the air; the annual maximum in September, one month after that for the air. The correspondence of the annual mean temperature of the soil at 6 feet with that of the air to within 1° is here confirmed: $61.6° - 1° = 60.6°$, as compared with 60.8°, the mean of the air readings.

HUMIDITY AND FOG.

The humidity record for Cinchona consists of daily readings of stationary wet and dry bulb thermometers at 7 a. m. and 3 p. m. A number of comparisons of wet-bulb readings with sling psychrometer readings were made in 1906 and 1909, showing that the wet-bulb readings are as a whole from 1.5 to 3 per cent too high, owing to the stationary character of the wet-bulb apparatus. Table 5 gives the monthly means

TABLE 5.

Month.	Per cent.	Month.	Per cent.
January	84.1	July	79.6
February	83.1	August	80.4
March	83.9	September	84.4
April	83.4	October	88.9
May	85.2	November	86.0
June	84.8	December	86.3
		Year	84.1

for fifteen years (1891 to 1905, inclusive), the mean of the two daily readings being taken as the daily mean. The reduction to percentages has been made with a table prepared by Mr. W. Maxwell Hall, and no correction for the inherent error of the instrument has been made.

A general correspondence may be seen, as is to be expected, between the annual curve of humidity and that of rainfall (fig. 1).

The high humidities prevalent at Cinchona and throughout the Blue Mountains are due in great part to the high percentage of cloudiness and the frequency of fog. On the northern slopes of the range at all elevations from below 4,500 feet to the summits of the highest peaks fog is prevalent from 10 a. m. to 4 p. m. on a very high percentage of the days in all months except February, July, and August. On the southern slopes the amount of fog is much less. Fog at night is rather exceptional, occurring more often, in my own observation, on the summits of the Main Ridge than below 5,800 feet.

RAINFALL.

The rainfall readings at Cinchona have been made from a Negretti and Zambra gauge of the ordinary type from day to day as the fall required. Those at New Haven Gap and Blue Mountain Peak were made on the last day of each month, no allowance being made for

evaporation. Table 6 gives the monthly means of rainfall for these three localities, those for Cinchona being based on records for thirty-nine years (1871 to 1909 inclusive); those for New Haven Gap on fourteen years (1882 to 1895, with twenty-four single months missing); those for Blue Mountain Peak on nineteen years (1890 to 1898, with nine months missing):

The data for the three mountain stations show an abundant rainfall at all seasons, but a fall which is not great as compared with such localities as Colon, Panama (112.6 inches), Kamerun (151.2

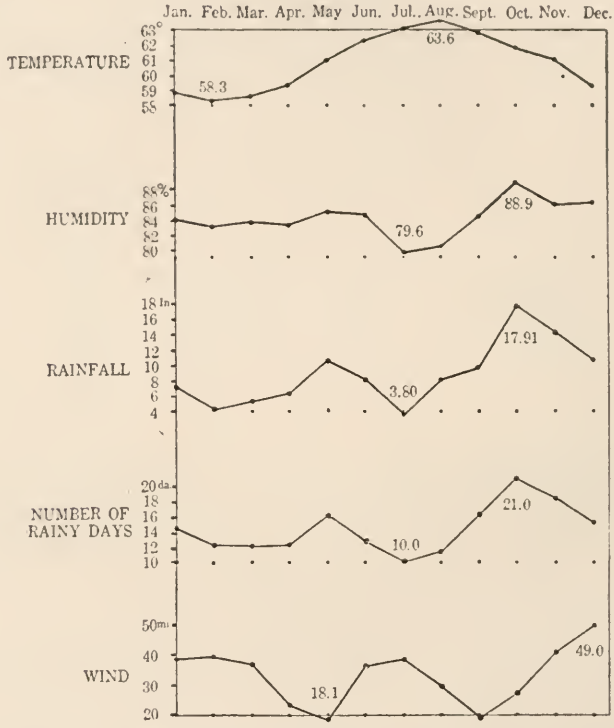


FIG. 1.—Annual curves of monthly means of principal elements of the climate at Cinchona.

inches), Sierra Leone (124 inches), and Ratnapura, Ceylon (149.7 inches). There is a pronouncedly heavier fall in May and in the late autumn and early winter months, whereas the lightest falls of the midsummer are seldom low enough to cause serious damage to other than the most hygrophilous vegetation. At Cinchona the annual maximum is reached in October, the minimum in February; at New Haven Gap the maximum is in December, the minimum in March; at Blue Mountain Peak they are in November and March respectively. There is an extreme degree of variability in the rainfall from year to year

Mountain bridle path traversing Windward Ravine Forest at 5,000 feet elevation. The tree fern is *Cyathea pubescens*.

and month to month. At Cinchona the highest annual falls were 108.12 inches in 1877 and 178.77 inches in 1909, the lowest 59.46 inches in 1897. In October the fall has been as heavy as 43 inches in 1904 and as light as 2.67 inches in 1891. In February the fall has been as great as 12.72 inches in 1893 and as little as 0.83 inch in 1903. The average departures from the mean for February and October for thirty-five years are

TABLE 6.—*Monthly mean rainfall for Cinchona, New Haven Gap, and Blue Mountain Peak.*

	Jan.	Feb.	Mar.	Apr.	May.	June.	July.
Cinchona	7.08	4.01	5.23	6.16	10.68	8.11	3.80
New Haven Gap	15.21	7.44	7.28	9.13	11.32	9.21	5.90
Blue Mountain Peak	11.96	10.41	6.57	11.56	14.25	12.77	9.37
Resource (1 mile south of Cinchona, elevation 3,700 feet)							
Port Antonio, (sea-level, north coast)							
Kingston (sea-level, south coast)							

	Aug.	Sept.	Oct.	Nov.	Dec.	Total.	
						Inches.	Cm.
Cinchona	8.04	9.73	17.91	14.29	10.66	105.70	268.5
New Haven Gap	4.78	6.36	20.05	15.67	24.28	113.85	289.0
Blue Mountain Peak	8.59	9.89	22.11	27.95	22.59	168.02	426.8
Resource (1 mile south of Cinchona, elevation 3,700 feet)						67.80	172.2
Port Antonio (sea-level, north coast)						130.48	331.5
Kingston (sea-level, south coast)						37.96	96.4

respectively 2.52 inches (for a mean of 4.01) and 9.93 inches (for a mean of 17.91). At New Haven Gap during April, May, and June 1892 there was not a measurable amount of precipitation, while during these months in 1894 there were 62.02 inches of rain.

The number of days per month at Cinchona on which there was a fall of 0.01 inch or more is exhibited in table 7, being the means of eighteen years (1892 to 1909 inclusive):

TABLE 7.—*Monthly mean number of rainy days.*

Month.	Days.	Month.	Days.
January	14.5	July	10.0
February	12.3	August	11.4
March	12.2	September	16.2
April	12.2	October	21.0
May	16.1	November	18.4
June	12.8	December	15.3
		Year	172.4

There is no other form of precipitation than rain, hail and snow being unknown, although the former occurs at rare intervals in the lowlands. The precipitation is either in the form of light showers of brief duration or prolonged but gentle downpours particularly characteristic of the May and winter rainy seasons and not uncommon at night during the winter. There is never, so far as I have observed and can learn, the hard downpour of large raindrops characteristic of tropical lowlands. The frequency of showers too light to register 0.01 inch is high, and they are not without influence on the vegetation. Although the number of rainy days is great and the frequency of light showers is high, yet the bulk of the annual rainfall is registered during the prolonged downpours. In the 168 months of 1892 to 1905 inclusive, there were 23 (14 per cent) in which 50 per cent or more of the monthly total fell upon one day; 64 (38 per cent) in which it fell upon two days; 45 (27 per cent) in which it fell upon three; and 36 (21 per cent) remaining in which it was more evenly distributed. The heaviest single daily falls of rain at Cinchona were 28.66 inches on May 25, 1898; 11.50 inches on August 10, 1903 (accompanying the hurricane which visited the island on that date), and 18.30 inches on November 8, 1909.

Dew is formed abundantly in open situations on clear nights at all seasons of the year.

SUNSHINE AND CLOUDINESS.

No indication of the relative amounts of sunshine and cloudiness is given by the figures exhibiting the number of rainy days, owing to the high frequency of foggy or cloudy days on which there is not an appreciable amount of precipitation. No records of sunshine have been kept at Cinchona by the Department of Public Gardens and Plantations. From November 1905 to March 1906 I kept a rough record of the number of hours of sunshine by observing the time at which it clouded over every day, and by estimation of the number of hours of sun during the part of the day when it is intermittently cloudy. My figures are shown in table 8, expressed in percentages of the total possible hours of sunshine.

TABLE 8.—*Average percentage of sunshine, Nov. 1905 to Mar. 1906.*

Month.	Per cent.
November	28
December	16
January	21
February	29
March	27
Mean	24

Interior of Windward Slope forest at 5,000 feet elevation. Left, *Podocarpus urbanii;* upper right, *Guarea swartzii;* lower right, *Beslevia lutea* and *Chusquea abietifolia;* bottom, *Blechnum capense.*

During these months the number of totally clear days was 6, the number of totally cloudy or rainy days was 50, the number of partially cloudy days 95. The total rainfall for these five months was 37.07 inches as contrasted with the mean of 41.27, while the number of rainy days was 74, the mean number being 72.7. This is partial, if not absolutely conclusive evidence that the above percentages are not below the normal.

The typical course of the day's weather is: clear from sunrise until 9 to 11 a. m., intermittently or entirely cloudy until nearly sunset, with two to three hours of fog in the mid-day or early afternoon, the sun setting clear. Rain usually occurs in the mid-day or early afternoon and the night is clear. During the summer months the percentage of sunshine is much greater than in the months tabulated above, but is so intermittent that it would be impossible to determine its percentage of the total number of hours without the use of appropriate instruments.

WIND.

The wind at Cinchona is prevailingly from the east and northeast and commonly reaches its highest force at night and in the winter season. Its influence on the vegetation is greatest on the peaks and ridges, and the fact that the lowest humidities accompany high wind may make its desiccating influence considerable. The monthly mean velocities of the wind in miles per day at Cinchona for eight years (1892 to 1899 inclusive), as measured by a Negretti and Zambra anemometer, are shown in table 9. The annual curve shows little save the lower rate in the rainy months (fig. 1).

TABLE 9.—*Monthly mean wind velocity.*

Month.	Velocity.	Month.	Velocity.
January	38.1	July	37.7
February	39.2	August	29.4
March	36.2	September	18.4
April	23.2	October	27.4
May	18.1	November	40.6
June	36.8	December	49.0

The annual mean daily velocity: 32.8 miles per day.

THE FLORA OF THE RAIN-FOREST.

Throughout the long history of the botanical exploration of Jamaica the flora of the Blue Mountains has received attention from numerous collectors, as well as from several systematists who have never visited the island. Among the earlier students were Swartz, Browne, Jacquin, Macfadyen, Purdie, M'Nab, Prior, and Marsh. More recently the activity of the Department of Public Gardens and Plantations, for a number of years located at Cinchona, in cooperation with the botanical gardens at New York and Berlin, has added considerably to a knowledge of the flora. At the present time these mountains may be looked upon as botanically well known, except in their less accessible parts to the north and northeast of Blue Mountain Peak.

The only comprehensive systematic work available for the Blue Mountain area is Grisebach's Flora of the British West Indies (1864). Since its appearance a number of new species from the region have been described in the Symbolæ Antillanæ, by Urban and his co-workers, and in the Bulletin of the Torrey Botanical Club by Britton. For the ferns an excellent manual exists in Jenman's Synoptical List of the Ferns and Fern-Allies of Jamaica,[1] since the publication of which a number of new fern species have been described from the region by Underwood and by Maxon. I have depended for my knowledge of the flora on the above-mentioned works, and on the determinations of my own collections, which have been made in part by Dr. N. L. Britton and Mr. W. Ralph Maxon, to whom most grateful thanks for this service are here returned, and in part by Mr. William Harris, who possesses more complete first-hand knowledge of the region than any other botanist.

I have not been concerned with a complete listing of the flora, but have endeavored to secure accurate determinations of all species which go to make up the characteristic features of the vegetation. In order to bring together in taxonomic sequence, with author names, all the plants mentioned in the description of the vegetation, the following list is given. The sequence is that of the Natürlichen Pflanzenfamilien; the nomenclature for Pteridophytes is in accordance with Christensen's Index Filicum, and the names for the Phanerogams have been brought into agreement with the Vienna code through the kindness of Dr. I. Urban. In the Pteridophytes the synonyms given in parentheses are those used in Jenman's List; in the Phanerogams those of the names occurring in Grisebach's Flora and Fawcett's List which are now obsolete have been given as synonyms, to which are added some names of extra-Jamaican forms, to which the Jamaican species were erroneously referred by early workers.

[1]Jenman, Synoptical List of the Ferns and Fern Allies. Bull. Dept. Pub. Gardens and Plant. Jamaica.

Mountain bridle path traversing Ridge Forest at 5,000 feet elevation in vicinity of Moree's Gap. The overhanging trees are *Cyrilla racemiflora* and *Clusia hæretioides*.

List of Characteristic Species.

PTERIDOPHYTA.

Hymenophyllaceæ.
- Trichomanes reptans Sw.
- Trichomanes hookeri Presl. (Trichomanes muscoides Sw.)
- Trichomanes crispum L.
- Trichomanes pyxidiferum L.
- Trichomanes capillaceum L. (Trichomanes trichoideum Sw.)
- Trichomanes scandens L.
- Trichomanes radicans Sw.
- Trichomanes rigidum Sw.
- Hymenophyllum tunbrigense (L.) Sm.
- Hymenophyllum fucoides Sw.
- Hymenophyllum polyanthos Sw.
- Hymenophyllum axillare Sw.
- Hymenophyllum crispum H. B. K.
- Hymenophyllum hirsutum (L.) Sw.
- Hymenophyllum sericeum Sw.

Cyatheaceæ.
- Balantium coniifolium (Hook.) J. Sm. (Dicksonia coniifolia.)
- Cyathea pubescens Mett.
- Cyathea tussacii Desv.
- Cyathea insignis Eaton.
- Cyathea harrisii Underw.
- Cyathea furfuracea Bak.
- Alsophila quadripinnata (Gmel.) C. Chr. (Alsophila pruinata Kaulf.)

Polypodiaceæ.
- Dryopteris hirta (Sw.) O. Kze. (Nephrodium hirtum Hook.)
- Dryopteris effusa (Sw.) Urban. (Nephrodium effusum Bak.)
- Polystichum plashnickianum (Kze.) Moore.
- Polystichum struthionis Maxon.
- Polystichum denticulatum (Sw.) J. Sm.
- Nephrolepis cordifolia (L.) Presl.
- Odontosorea aculeata (L.) J.Sm. (Davallia aculeata Sw.)
- Dennstædtia dissecta (Sw.) Moore (Dicksonia dissecta Sw.)
- Diplazium celtidifolium Kze. (Asplenium celtidifolium Webb.)
- Diplazium costale (Sw.) Presl (Asplenium costale Sw.)
- Diplazium altissimum (Jenm.) C. Chr. (Asplenium altissimum Jenm.)
- Diplazium brunneo-viride (Jenm.) C. Chr. (Asplenium brunneo-viride Jenm.)
- Asplenium resiliens Kze.
- Asplenium obtusifolium L.
- Asplenium pteropus Kaulf.
- Asplenium alatum H. B. Willd.
- Asplenium lunularum Sw.
- Asplenium dimidiatum Sw.
- Asplenium cristatum Lam. (Asplenium cicutarium Sw.)
- Plagiogyria biserrata Webb.
- Blechnum attenuatum (Sw.) Mett. (Lomaria attenuata Willd.)
- Blechnum capense (L.) Schl. (Lomaria procera Spreng.)

PTERIDOPHYTA—Continued.

Polypodiaceæ—Continued.
- Blechnum tabulare (Thunb.) Kuhn. (Lomaria boryana Willd.)
- Blechnum occidentale L.
- Ceropteris tartarea (Cav.) Link. (Gymnogramme tartarea Desv.)
- Cheilanthes microphylla Sw.
- Hypolepis nigrescens Hook.
- Hypolepis pulcherrima Underw. & Maxon.
- Pteris longifolia L.
- Pteris podophylla Sw.
- Pteris deflexa Link.
- Histiopteris incisa (Thunb.) J. Sm. (Pteris incisa Thunb.
- Pteridium aquilinum (L.) Kuhn. (Pteris aquilina L.)
- Pæsia viscosa St. Hil. (Pteris viscosa Moore).
- Vittaria lineata (L.) Sm.
- Antrophyum lineatum (Sw.) Kaulf.
- Polypodium serrulatum (Sw.) Mett. (Xiphopteris serrulata Kaulf.)
- Polypodium myosuroides Sw. (Xiphopteris myosuroides.)
- Polypodium gramineum Sw.
- Polypodium marginellum Sw.
- Polypodium grisebachii Underw. (Polypodium exiguum Griseb.)
- Polypodium basiattenuatum Jenm.
- Polypodium induens Maxon.
- Polypodium cultratum Willd.
- Polypodium suspensum L.
- Polypodium taxifolium L.
- Polypodium plumula H. B. Willd.
- Polypodium polypodioides (L.) Hitch. (Polypodium incanum Sw.)
- Polypodium thyssanolepis A. Br.
- Polypodium loriceum L.
- Polypodium crassifolium L.
- Polypodium repens Aublet.
- Polypodium lanceolatum L.
- Elaphoglossum inæqualifolium (Jenm.) C. Chr. (Acrostichum inæqualifolium Jenm.)
- Elaphoglossum pallidum (Bak.) C. Chr. (Acrostichum pallidum Bak.)
- Elaphoglossum latifolium (Sw.) J. Sm. (Acrostichum latifolium Sw.)
- Elaphaglossum petiolatum (Sw.) Urb. (Acrostichum viscosum Sw.)
- Elaphoglossum cinchonæ Underw.
- Elaphoglossum hirtum (Sw.) C. Chr. (Acrostichum squamosum Sw.)
- Elaphoglossum villosum (Sw.) J. Sm. (Acrostichum villosum Sw.)

Gleicheniaceæ.
- Gleichenia jamaicensis (Underw.)
- Gleichenia bancroftii Hook.
- Gleichenia pectinata (Willd.) Presl.

Marattiaceæ.
- Marattia alata Sw.
- Danæa alata Sm.
- Danæa jamaicensis Underw.

List of Characteristic Species—Continued.

PTERIDOPHYTA—Continued.

Lycopodiaceæ.
- Lycopodium reflexum Lam.
- Lycopodium taxifolium Sw.
- Lycopodium cernuum L.
- Lycopodium clavatum L.
- Lycopodium fawcettii Lloyd and Underw. (Lycopodium complanatum L.)

GYMNOSPERMÆ.

Taxaceæ.
- Podocarpus urbanii Pilger (Podocarpus coriaceus Rich.)

Pinaceæ.
- Juniperus barbadensis L.

ANGIOSPERMÆ.

Gramineæ.
- Panicum glutinosum Sw.
- Olyria latifolia L.
- Danthonia shrevei Britton.
- Zeugites americana Willd.
- Chusquea abietifolia Griseb.

Cyperaceæ.
- Rynchospora eggersiana Boeckl. (Rynchospora florida Griseb.)
- Rynchospora elongata Boeckl.
- Rynchospora polyphylla Vahl.
- Uncinia hamata (Sw.) Urb. (Uncinia jamaicensis Pers.)

Araceæ.
- Anthurium scandens (Aubl.) Engl.

Bromeliaceæ.
- Tillandsia incurva Griseb.
- Tillandsia complanata Benth.
- Caraguata sintenesii Bak.

Liliaceæ.
- Smilax celastroides Kunth.

Orchidaceæ.
- Pleurothallis sp.
- Stelis ophioglossoides (Jacq.) Sw.
- Lepanthes tridentata Sw.
- Lepanthes concinna Sw
- Lepanthes concolor Fawc. and Rendle.
- Liparis elata Lindl.
- Calanthe mexicana Reichenb. f.
- Isochilus linearis (Jacq.) R. Br.
- Epidendrum cochleatum L.
- Epidendrum ramosum Jacq.
- Epidendrum verrucosum Sw.
- Dichæa trichocarpa Lindl.
- Dichæa graminea (Sw.) Griseb.
- Dichæa glauca Lindl.
- Spiranthes elata (Sw.) L. C. Rich.
- Physurus plantagineus (L.) Lindl.
- Physurus hirtellus (Sw.) Lindl.
- Prescottia stachyodes Lindl.

Piperaceæ.
- Piper geniculatum Sw.
- Piper fadyenii C. DC.
- Piper tuberculatum Jacq.
- Peperomia hispidula (Sw.) A. Dietr.
- Peperomia tenella A. Dietr.
- Peperomia glabella A. Dietr.
- Peperomia baselläefolia Kunth.

ANGIOSPERMÆ—Continued.

Piperaceæ—Continued.
- Peperomia obtusifolia var.
- Peperomia galioides Kunth.
- Peperomia filiformis A. Dietr.
- Peperomia verticillata (L.) A. Dietr.
- Peperomia reflexa (L. f.) A. Dietr.
- Peperomia turfosa C. DC.
- Peperomia rupigaudens C. DC.

Chloranthaceæ.
- Hedyosmum nutans Sw.
- Hedyosmum arborescens Sw.

Myricaceæ.
- Myrica microcarpa Benth

Urticaceæ.
- Pilea microphylla (L.) Liebm.
- Pilea parictaria (L.) Blume.
- Pilea parietaria var. alpestris Urb.
- Pilea grandifolia (L.) Blume.
- Pilea nigrescens Urb.
- Pilea brittoniæ Urb.
- Bœhmeria caudata Sw.
- Phenax hirtus (Sw.) Wedd.

Loranthaceæ.
- Loranthus parvifolius Sw.
- Phthirusa lepidobotrys (Griseb.) Eichl. (Loranthus lepidobotrys Griseb.)
- Dendrophthora cupressoides (Griseb.) Eichl. (Arceuthobium cupressoides Griseb.)
- Dendrophthora gracilis (Griseb.) Eichl. (Arceuthobium gracile Griseb.)
- Dendrophthora danceri Kr. and Urb.
- Phoradendron flavens Griseb.
- Eubrachion ambiguum var. jamaicense Kr. and Urb.

Amarantaceæ.
- Iresine celosioides L.

Lauraceae.
- Nectandra coriacea (Sw.) Griseb.
- Nectandra patens (Sw.) Griseb.

Papaveraceæ.
- Bocconia frutescens L.

Cunoniaceæ.
- Weinmannia pinnata L. (Weinmannia glabra L. f., Weinmannia hirta Sw.)

Rosaceæ.
- Rubus alpinus Macf.
- Fragaria vesca L.

Rutaceæ.
- Fagara hartii Kr. and Urb.

Simarubaceæ.
- Brunellia comocladifolia Humb and Bonpl.

Meliaceæ.
- Guarea swartzii DC. (Guarea trichilioides L.)

Euphorbiaceæ.
- Acalypha virgata L.
- Alchornea latifolia Sw.
- Mettenia globosa (Sw.) Griseb.

Cyrillaceæ.
- Cyrilla racemiflora L. (Cyrilla antillana Michx.)

List of Characteristic Species—Continued.

ANGIOSPERMÆ—Continued.

Aquifoliaceæ.
Ilex montana *var.* occidentalis Loes.
Ilex obcordata Sw.
Sapindaceæ.
Turpinia occidentalis Don.
Dodonæa angustifolia Sw. (Dodonæa viscosa L.)
Rhamnaceæ.
Rhamnus sphaerospermus Sw. (Frangula sphærocarpa Griseb.)
Malvaceæ.
Malvaviscus arboreus Cav.
Marcgraviaceæ.
Marcgravia brownei Urb.
Theaceæ.
Cleyera theoides (Sw.) Choisy.
Hæmocharis hæmatoxylon (Sw.) Choisy. (Laplacea hæmatoxylon Camb.)
Hæmocharis villosa (Macf.) Choisy. (Laplacea villosa Griseb.)
Guttiferæ.
Clusia havetioides Pl. and Triana. (Tovomita havetioides Griseb.)
Hypericaceæ.
Ascyrum hypericoides L.
Bixaceæ.
Xylosma nitidum (Hell.) A. Gray. (Myroxylon nitidum (Hell.) Kuntze.)
Passifloraceæ.
Passiflora sexflora Juss.
Passiflora peduliflora Berter.
Begoniaceæ.
Begonia nitida Dryand.
Begonia acuminata Dryand. (Begonia jamaicensis A. DC.)
Begonia scandens Sw.
Thymeleaceæ.
Daphnopsis tinifolia (Sw.) Griseb.
Myrtaceæ.
Eugenia fragrans (Sw.) Willd. (Myrtus fragrans Sw.)
Eugenia alpina (Sw.) Willd.
Eugenia marchiana Griseb.
Eugenia biflora var. wallenii Kr. and Urb.
Eugenia harrisii Kr. and Urb.
Psidium montanum Sw.
Melastomaceæ.
Meriania purpurea Sw.
Meriania leucantha Sw.
Miconia quadrangularis (Sw.) Naud.
Miconia rubens (Sw.) Naud. (Tamonea rubens Sw.)
Miconia rigida (Sw.) Triana. (Tamonea rigida Sw.)
Heterotrichum patens (Sw.) DC.
Mecranium purpurascens (Sw.) Triana.
Blakea trinervis L.
Araliaceæ.
Sciadophyllum brownei Spreng.
Gilibertia pendula (Sw.) E. March. (Dendropanax pendula Decne. and Planch.
Gilibertia nutans (Sw.) E. March. (Dendropanax nutans Sw.)
Gilibertia arborea (L.) E. March. (Dendropanax arboreum Decne. and Planch.)

ANGIOSPERMÆ—Continued.

Araliaceæ—Continued.
Oreopanax capitatum (Jacq.) Decne. and Planch.
Umbelliferæ.
Hydrocotyle pusilla Rich.
Cornaceæ.
Garrya fadyenii Hook.
Clethraceæ.
Clethra alexandri Griseb.
Clethra occidentalis (L.) Steud. (Clethra tinifolia Sw.)
Vacciniaceæ.
Vaccinium meridionale Sw.
Ericaceæ.
Lyonia jamaicensis (Sw.) Don.
Lyonia octandra (Sw.) Griseb.
Myrsinaceæ.
Rapanea ferruginea (R. & P.) Mez (Myrsine laeta A. DC.)
Wallenia venosa Griseb.
Wallenia crassifolia Mez.
Wallenia fawcettii Mez.
Sapotaceæ.
Dipholis montana (Sw.) Griseb.
Gentianaceæ.
Lisianthus latifolius Sw. (Leianthus latifolius Griseb.)
Asclepiadaceæ.
Metastelma fawcettii Schlecht.
Metastelma atrorubens Schlecht.
Metastelma ephedroides Schlecht.
Convolvulaceæ.
Ipomœa triloba L.
Borraginaceæ.
Tournefortia cymosa L.
Verbenaceæ.
Lantana camara L.
Citharexylum caudatum L.
Labiatae.
Micromeria obovata (W.) Benth.
Salvia jamaicansis Fawc.
Solanaceæ.
Solanum punctulatum Dun.
Acnistus arborescens (L.) Schlecht.
Datura suaveolens Humb. and Bonpl.
Cestrum hirtum Sw.
Cestrum sp.
Brunfelsia jamaicensis (Benth.) Griseb.
Brunfelsia harrisii Urb.
Solandra grandiflora Sw.
Gesneraceæ.
Gesnera mimuloides (Griseb.) Urb.
Columnea hirsuta Sw.
Besleria lutea L.
Rubiaceæ.
Manettia lygistum Sw.
Psychotria brownei Spreng.
Psychotria corymbosa Sw.
Palicourea crocea (Sw.) R. & S.
Relbunium hypocarpium (L.) Hemsl. (Galium hypocarpium Endl.)
Caprifoliaceæ.
Viburnum villosum Sw.
Viburnum alpinum Macf. (Viburnum glabratum H. B. K.).

List of Characteristic Species—Continued.

ANGIOSPERMÆ—Continued.

Cucurbitaceæ.
Cionosicys pomiformis (Macf.) Griseb.
Campanulaceæ.
Lobelia martagon (Griseb.) Hitch. (Tupa martagon Griseb.)
Lobelia assurgens L. (Tupa assurgens (L.) DC.)
Lobelia caudata (Griseb.) Urban. (Tupa caudata Griseb.)
Compositæ.
Vernonia divaricata Sw.
Vernonia intonsa Gleason.
Vernonia arborescens Sw.
Eupatorium dalea (L.) DC.

ANGIOSPERMÆ—Continued.

Compositæ—Continued.
Eupatorium critoniforme Urb.
Eupatorium parviflorum Sw.
Eupatorium lucidum Ort.
Eupatorium corylifolium Griseb.
Baccharis scoparia Sw.
Bidens coreopsidis DC.
Bidens shrevei Britton.
Liabum umbellatum (L.) Sch. Bip. (Liabum brownei Cass.)
Senecio swartzii DC.
Senecio fadyenii Griseb.
Senecio laciniatus (Sw.) DC.

THE VEGETATION OF THE RAIN-FOREST.

ECOLOGICAL CHARACTERISTICS OF THE RAIN-FOREST.

The peaks and highly-eroded slopes of the Blue Mountains, in the absence of cliffs and rock outcrops of any considerable size, and in the lack of any disturbance by man, exhibit a forest covering of striking continuity. (See upper slopes of range in plate 5). The color tone of the landscape is a dull mingling of darker shades of green, with a blending of gray on the ridges, where *Usnea* is common in the open tree tops. Neither among the forest trees nor the smaller constituents of the vegetation are there any conspicuous colors of leaf or flower. *Clethra occidentalis* occurs in sufficient abundance for its racemes of white flowers to be a somewhat noticeable feature of the autumn landscape, and at the same season the large yellow flowers of *Bidens shrevei* cover the crown of trees into which it has climbed, and touches of red are here and there given the forest by the autumn coloration of the two species of Viburnum. The only other showy bloomers of the arboreal flora are *Hæmocharis hæmatoxylon* and *Meriania purpurea*. In the former the flowers are white and in the latter a deep red, and when the two are in bloom simultaneously in the spring they give a touch of color to the otherwise dull landscape. In the interior of the heaviest rain-forest there is an almost utter absence of colors other than green, which with the absence of showy birds and insects gives the forest an air of gloom to which its continual fogginess only adds.

There are no gigantic trees towering above the general level of the forest, and indeed the stature of the trees is surprisingly small in view of the apparent favorableness of the rainfall and temperature conditions. In ravines they may attain to a height of 60 feet, but on the ridges, particularly those at high altitude, the largest individuals of *Podocarpus* and *Clethra* seldom exceed 20 feet in height. The combined influences of wind and occasional low water content of the soil may contribute to the low stature of the trees of the ridges at higher altitudes, but in general the phenomenon is due to the rapidity of erosion.

Nearly all the trees on slopes, even many young ones, show a leaning down hill (see plate 12), larger ones are often bent over nearly to the horizontal, while the number of down-fallen trunks, all pointing down hill, indicates only too clearly the destructive influence of erosion on the older trees. Only along the beds of valleys where the soil is relatively stable have I seen trees of more than 30 inches (76 cm.) trunk diameter, these usually being *Solanum punctulatum* or *Gilibertia arborea*.

The forests of the Blue Mountains exhibit an intermingling of temperate and tropical characteristics both in their composition and their general ecology. I made no exact determinations of the composition of the forest because of the impossibility of securing satisfactory data where the rapidity of erosion causes so many complications in the forest stand. However, rough estimations which I made in a number of localities indicated that *Clethra occidentalis*, *Vaccinium meridionale*, and *Podocarpus urbanii* form about 50 per cent of the stand and that an additional 35 per cent is made up of some 10 other species, as follows: *Alchornea latifolia*, *Cyrilla racemiflora*, *Ilex montana* var. *occidentalis*, *Guarea swartzii*, *Brunellia comocladifolia*, *Clusia havetioides*, *Gilibertia arborea*, *Rapanea ferruginea*, *Solanum punctulatum*, and *Eugenia biflora* var. *wallennii*. In other words, the general character of the composition is that of temperate forests rather than of those in tropical lowlands. The examinations which I have made of virgin lowland forests in the valley of the Mabess River in the northeastern part of Jamaica and in the vicinity of Mount Diablo, in the central part, make me quite confident in stating that they are far more complex in their composition than the mountain forests and more so than the forests of the Philippine Islands which have been described by Whitford.[1] The constant overturning of the largest trees by erosion gives opportunity for the entrance of young individuals, and results in a great diversity in trunk diameters. *Clethra*, *Vaccinium*, and *Podocarpus* all sucker freely from old roots and trunks, so that a single root system often anchors a thick horizontal trunk and several young vertical ones, which adds still further to this diversity.

The individual trees are mostly of temperate rather than of tropical type in the order of branching and shape of the crown. In *Vaccinium*, *Podocarpus*, *Clethra*, *Ilex*, and other common forms the order of branching varies from the seventh to the ninth, or is even higher; in *Brunellia comocladifolia* alone is there a low order—the fourth. In *Rapanea ferruginea* the lateral branches exceed the main trunk in growth; in *Brunellia* there is a lax, open crown, and in *Eugenia fragrans* and *Eugenia alpina* there are round compact heads of foliage. With these exceptions there are no trees which present any peculiarities of form. The bark is universally smooth and thin. Cauliflory does not occur,

[1] Whitford, H. N. The Vegetation of the Lamao Forest Reserve. Philip. Jour. Sci., I, 373–431, 637–682, 1906.

but is simulated in several species in which the flowers are produced from the axils of the fallen leaves of the preceding year, as in *Eugenia marchiana*, *Acnistus arborescens*, *Mecranium purpurascens*, and *Alchornea latifolia*. Such purely tropical characteristics as plank buttresses and the bunching of leaves at the ends of the branches are entirely absent. The attenuated leaf ends—or "dripping points"—which have been found to characterize the rain-forests of the eastern hemisphere, are very uncommon in the Jamaican rain-forest, and the functional value of such structures appears to have been overestimated.[1]

Only in the narrowest ravines is there a lofty and closed canopy, and as one proceeds into wider ravines and from them onto slopes and finally onto the ridges the canopy becomes more and more open, although its general level is more uniform on the ridges than in the ravines. The canopy itself has no line of demarcation from the foliage of the under-trees and shrubs, resulting in an irregular and more or less solid mass of foliage from the tree tops down nearly to the level of the terrestrial herbaceous plants. There is, however, just above the herbaceous vegetation a layer free of foliage, which in wide ravines sometimes reaches as high as 10 or 20 feet (3 to 6 meters), but on the slopes and ridges disappears altogether.

The leaves of the generality of trees and shrubs are of medium or small size, from about 75 sq. cm. in area in *Clethra alexandri* to less than 1 sq. cm. in *Eugenia alpina* (see plate 21 A). In all but three of the commonest trees (*Brunellia*, *Weinmannia*, and *Guarea*) the leaves are simple, and without exception they are firm or even coriaceous, with from one to four layers of greatly elongated palisade cells and with compact mesenchyma, in high contrast to the extremely hygrophilous character of the leaves of the ferns and other herbaceous plants of the forest floor.

The floor of the rain-forest is covered with a litter of leaves, twigs, and limbs, the decay of which seems to be retarded rather than accelerated by the extreme wetness maintained at relatively low temperatures. Ants do a small amount of work in destroying dead trees before they fall, and an abundance of small discomycetous fungi (almost the only representatives of their group) hastens the disintegration of the leaves and small twigs. The soil is extremely rich in organic matter, but is shallow and full of angular rock fragments.

The terrestrial herbaceous vegetation varies from extreme wealth in the ravines to almost complete absence in many places on the ridges where the climbing bamboo, *Chusquea abietifolia*, is abundant, and where the amount of light reaching the forest floor is so great as to permit the development of extended thickets of the scrambling ferns *Gleichenia* and *Odontosorea*. In the ravines ferns form by far the most

[1]Shreve, Forrest, The Direct Effects of Rainfall on Hygrophilous Vegetation. Jour. of Ecology, 2, 1914.

A Windward Ravine enveloped in the usual mid-day fog. The shrubs are species of *Piper* and *Bochmeria;* the tree-fern is *Cyathea insignis;* against the sky hang festoons of the climber *Marcgravia brownei*.

prominent part of the herbaceous vegetation, with species of *Pilea* and *Peperomia* in the minority and terrestrial orchids not abundant. Species of *Rynchospora* and the endemic sedge *Uncinia hamata* are not infrequent in more open situations, but the sedge and grass types are uncommon on the whole, as are also monocotyledonous plants in general. The absence of palms and of the musaceous type of large-leaved phanerogams in general, taken together with the presence of tree-ferns and filmy ferns and the general predominance of bryophytes and pteridophytes, marks the salient features of this type of rain-forest.

In the abundance of its epiphytic vegetation the rain-forest is tropical in character. Tank epiphytes of the bromeliaceous type are common, although represented by but few species; large woody forms are not frequent. Orchids, with either water-storing leaves or storing roots, are common, but are not so frequent as the ferns, which range from large hygrophilous forms to small xerophilous ones, including notably a number of species of Hymenophyllaceæ. A large part of the bulk of the epiphytic vegetation is made up of mosses and hepatics, which serve as a water-retaining substratum for the larger forms.

The representation of lianes is poor, particularly outside the ravines, where *Marcgravia* and several asclepiadaceous forms occur together with the low-growing climbing ferns, species of *Polypodium* and *Blechnum*. The scrambler *Chusquea* is abundant in the open forest of slopes and ridges.

The continuity of the forest formation is broken by occasional landslips and by the thickets of scrambling ferns along the ridges and on the highest peaks. On the northwestern face of Sir John Peak, near its summit, and on the same face of Mossman's Peak are also patches of a coarse bunch-grass (*Danthonia shrevei*), which has not been collected elsewhere in the island. It grows in large hummocks (see plate 19), and is accompanied by scattering plants of *Gleichenia*, with dwarf individuals of *Clethra alexandri*, *Ilex obcordata*, and *Weinmannia pinnata* about the edges. The areas are not old landslips, the character of their soil is not peculiar, neither are they exposed to conditions any more adverse to tree growth than those operative on the peaks themselves. It is impossible to gain any notion whether the areas are encroaching on the forest. The habit of the grass is such as to cover and completely shade the ground, and seedlings of other plants are rare between the hummocks. The rapidity of the erosion now going on makes it highly probable that in recent geological time the Blue Mountains extended considerably above their present altitude. At a time when these two peaks were loftier they would, in all probability, have borne alpine grassland above the tree limit, such as Volkens[1] encountered on Kilimandjaro at 7,800 feet, less than 400 feet higher than the summit of Blue Mountain Peak, and at 15° lower latitude.

[1]Volkens, G., Der Kilimandscharo. Berlin, 1897.

These considerations lead me to the surmise that the patches of *Danthonia* on Sir John Peak and Mossman's Peak are relicts of a former extensive alpine grassland formation which has been encroached upon by the forest as the mountains have been worn down below the tree limit.

HABITAT DISTINCTIONS IN THE RAIN-FOREST.

An examination of the forest formation which clothes the Blue Mountain range reveals both vegetative and floristic differences in its character in different localities. These differences are due (1) to the climatic difference between the northern, or windward, and the southern, or leeward, slopes of the range, which has its basis in differences in precipitation and the number of hours of fog and sunshine; (2) to local differences due to the highly dissected erosion topography, which have their basis in differences of atmospheric humidity and wind action; (3) to the altitude, which has its basis partly in temperature differences. The marked climatic difference between the northern and southern slopes, due to the prevailing direction of the trade wind, operates in a manner and direction such as to obscure any influence which the direction of slope in relation to insolation might have in differentiating the conditions for vegetation on the north and south slopes of the range. The low latitude of Jamaica makes this a factor which would not be operative in any case for more than a few months in winter. In like manner the striking difference in conditions of atmospheric humidity between the bottoms of ravines and the summits of ridges tends to obscure any influence which differences in amount of soil moisture might have in these habitats during the relatively dry periods which occasionally supervene. In view of the excellent distribution of the rainfall I feel confident in stating that the fluctuating amounts of soil moisture are a negligible factor in the distribution of vegetation. During the very exceptional dry periods, such as that which has been mentioned as occurring at New Haven Gap in April, May, and June, 1892, the depression of soil-moisture content would no doubt be sufficient to defoliate, if not to kill, the most hygrophilous shrubs and herbaceous plants, particularly as such a rainless period would be one of high percentage of insolation, high temperatures, and low humidity.

The differences in temperature which exist between sea-level and 4,500 feet are profoundly significant to vegetation. The smaller difference which exists between the 4,500 feet (1,372 meters) level and the summits of the three highest peaks is of no such importance, although it appears to be responsible for the limiting of the vertical distribution of many species. During the day the uniformity of moisture conditions on the windward slopes from 4,500 to 7,400 feet (2,250 meters) tends to offset the most important of the temperature influences, that is, on

Interior of forest at New Haven Gap which is identical with that in Windward Ravines. The pendant moss is *Phyllogonium fulgens;* the climbing fern, *Blechnum attenuatum;* the large-leaved shrub, *Bochmeria caudata.*

transpiration and growth. Indeed, the temperature conditions on the windward slope between the altitudes mentioned are made more uniform than on the leeward slope by the fact that much of the dynamic cooling of the air driven up from the near-by coast goes into the condensation of moisture. The differences of altitude that exist within our area are accompanied by negligible differences in rainfall and cloudiness. The leeward slopes, however, get a somewhat higher rainfall just below the Main Ridge than at lower altitudes, which is true no matter at what altitude on the Main Ridge, and is merely due to precipitation from clouds which are carried beyond the crest of the ridge by wind.

The sets of factors indicated do not operate independently, neither do the different habitats fail to shade into one another in the character of their vegetation. Deep ravines on the leeward slope resemble in many respects less deep ones on the windward side; peaks and ridges at lower altitudes resemble those at higher altitudes; ridges which are at the same time gaps resemble ravines more than they do the more exposed ridges. The ravines vary in width and depth, according to their age; when followed upward they broaden and emerge into the upper slope of the valley to which they are tributary.

The ravines and valley bottoms and their adjacent slopes will be shown to be the most hygrophilous habitats in the rain-forest; particularly on the windward slope they show a wealth and luxuriance which rival that of the lowland forests, together with the predominance of bryophytes and pteridophytes, which is the strongest characteristic of the region.

The following sections embrace a brief descriptive account of the vegetation of the Blue Mountain region. The habitats under which the descriptions are grouped have been distinguished in accordance with the conditions just discussed. The most important distinction within the region is that between the two slopes of the range, which are designated the Windward and Leeward rather than the Northern and Southern, in order to emphasize the fact that it is the climatic difference between them due to the trade wind and not the chance fact of their geographical orientation which is critical. Second in importance as a distinguishing factor is the topography, which leads to a subdivision of the two main slopes into ravines, slopes, and ridges. The fact that the differences between the ridges of the Windward and Leeward slopes are negligible has led to their combined treatment. The extreme summits of Blue Mountain and Sir John Peaks are treated separately, and the epiphytes have also been given special treatment, because their occurrence and distribution are more dependent upon vertical differences of conditions within the rain-forest than on the horizontal differences between the habitats recognized.

The Windward Ravines exhibit to the most striking degree the characteristics of the rain-forest, and the other types have been treated

from the point of view of their departure from them. So far as concerns their relative area, the Slope Forests far exceed the other types, but their characteristics and vegetation are intermediate between those of the ravines and the ridges, and they do not possess the interest of either of the latter habitats.

WINDWARD RAVINES.

The ravines and valley bottoms of the Windward Slopes exhibit to the highest degree all those features of vegetation and climate which find expression in the term "rain-forest," although they exhibit quite as strongly as do the other habitats the montane features which distinguish the entire region from the lowland rain-forests. In the ravines, at least, are trees of stately size, forming a more or less continuous canopy beneath which under-trees and shrubs form thickets varying in density according as the main forest canopy is more or less open. The floor of the forest is covered with terrestrial ferns or flowering plants, which, in turn, vary in their stand with the density of the shrubbery and under-trees above them. Throughout the lower levels of the forest garlands of golden-brown mosses—species of *Phyllogonium* and *Meteorium*—clothe the large trunks and hang from every twig in the undergrowth. On leaning trunks and horizontal limbs are crowded colonies of epiphytic ferns, orchids, and other flowering plants, from which hang pendant fronds of *Hymenophyllum* or *Elaphoglossum*. In one spot the terrestrial herbaceous vegetation will far exceed the epiphytic; in another masses of epiphytes may be found growing above a nearly bare forest floor, or again the epiphytes may be crowded out by the profuse growth of the climbing *Marcgravia*. Tree-ferns are abundant, standing singly or in groups, either beneath the shade of the largest trees or exposed to the sky. Their trunks form the support for climbing ferns and for masses of the most hygrophilous of the filmy ferns.

A rather limited number of species of trees and shrubs, together with a relatively small number of herbaceous flowering plants, mingle with a large number of ferns, lycopods, mosses, and hepatics to constitute a type of forest which is far less rich in species and somewhat less rich in individuals than the best-developed lowland rain-forest. Varying greatly from spot to spot in the arrangement of its component species, the forest also exhibits a common tropical characteristic in the abundance in one spot of a species which may be rare for miles around.

No picture of the Leeward Ravine forests is complete which does not portray the floating fog, in which it is enveloped so much of the time, and the reeking wetness which keeps its pads of mosses and hepatics always saturated and its foliage continously wet for days at a time. The height and constancy of the atmospheric moisture are the most

Looking over the canopy of Windward Ravine Forest in the vicinity of Morce's Gap.

potent factors in determining the character of the vegetation of the ravines, as well as in differentiating them from other habitats. Caused primarily by the abundant and well-distributed rainfall, as well as the prevalent fog, the humidity is maintained through the immense evaporating surface provided by the litter on the ground, the wet foliage, and the sponge-like masses of hepatics and mosses. Sheltered by the winds which sweep over the ridges and peaks, the Ravines are protected also from the mid-day rise of temperature, both through the uppermost layers of foliage and through the fogginess, by virtue of which conditions the constancy of the high humidity is almost unbroken. Influences which tend to lower the humidity, and which operate through only a few hours, are offset by an increased rate of evaporation from the wet surfaces. Continued prevalence of such conditions through many days, however, serves to lower the humidity at the forest floor, with results fatal to many of the terrestrial herbaceous plants and the more hygrophilous epiphytes, as I had opportunity to observe in April 1903, after three months with a rainfall of 3.45 inches (8.7 cm.), in which the normal fall is 16.32 inches (41.5 cm.). Coupled with the high humidity are temperature conditions of great constancy, the daily range varying from 5.8° to 7.6° F.

The top of the Ravine forest, as seen from the adjacent slopes, presents an irregularity of surface much greater than that of the Slope and Ridge forest; the largest trees standing well apart from each other, bearing crowded masses of epiphytes, and festooned with pendant mosses, while between them the canopy is formed by the crowns of smaller melastomaceous or rubiaceous under-trees or groups of tree-ferns. This irregularity of the canopy is due to the downfall through erosion of some of the largest trees and the slowness of the growth of the younger trees by which they will be replaced ultimately. The largest of the trees found only in Ravines are *Solanum punctulatum*, *Guarea swartzii*, *Hedyosmum arborescens*, and *Turpinia occidentalis*, while together with them grow trees more frequent on the slopes, such as *Hæmocharis hæmatoxylon*, *Alchornea latifolia*, *Meriania purpurea*, *Ilex montana* var. *occidentalis*, *Lyonia jamaicensis*, and *Clethra occidentalis*. The under-trees of the ravine forest are species which never reach the size of those just mentioned, and grow either in their shade or else themselves form the canopy of the forest. The commonest of them are *Mecranium purpurascens*, *Bœhmeria caudata*, *Palicourea crocea*, *Psychotria corymbosa*, *Eugenia biflora* var. *wallennii*, *Cestrum hirtum*, and *Miconia rubens*. With these grow the tree-ferns, the commonest of which are *Cyathea pubescens*, *Cyathea tussaccii*, *Cyathea furfuracea*, and *Cyathea insignis*. A number of smaller under-trees and shrubs are equally characteristic of the lower layers of the ravine forest, notably *Piper geniculatum*, *Piper fadyenii*, *Tournefortia cymosa*, *Datura suaveolens*, *Acalypha virgata*, *Besleria lutea*, and *Senecio swartzii*.

The terrestrial herbaceous vegetation varies more with the physiographic age of the ravine than does the arborescent vegetation, the initial ravines, with steep sides and rocky floor, differing from the sequential ones with more open sides and a deeper soil. The beds of steep and narrow ravines are often covered with coarse stones to so great a depth as to be almost devoid of large herbaceous plants, yet the stones themselves are covered with *Monoclea* or with mats of *Pallavicinia*, *Riccardia*, or *Plagiochila*, together with small filmy ferns, such as *Trichomanes pyxidiferum*, *Trichomanes reptans*, and *Trichomanes hookeri*. A few small flowering plants of pronouncedly hygrophilous character also occur in rocky ravines and on the steepest slopes that are deeply shaded, as *Peperomia hispidula*, *Peperomia filiformis*, *Hydrocotyle pusilla*, *Pilea brittoniæ*, and *Gesnera mimuloides*.

The beds of somewhat wider ravines provide soil of sufficient depth to support a dense growth of coarse ferns (see plate 2). The commonest and most wide spread species of ferns in such situations are *Diplazium celtidifolium*, *Diplazium costale*, *Asplenium alatum*, *Dennstædtia* sp., *Diplazium altissimum*, *Diplazium brunncoviride*, *Danæa jamaicensis*, *Asplenium rhizophorum*, and *Marattia alata*, and with them grow less frequently or more sporadically a large number of other species. The wider and more shallow ravines have a less number of ferns in their herbaceous vegetation and a greater number of flowering plants, notably *Pilea nigrescens*, *Peperomia turfosa*, *Peperomia obtusifolia*, and *Pilea parietaria*, together with the less frequent *Physurus hirtellus*, *Calanthe mexicana*, *Prescottia stachyodes*, and *Liparis elata*.

The trunks and limbs of the massive trees of the Windward Ravines bear a profuse epiphytic vegetation, which will be treated under a later heading. A small number of species of lianes are present, which are far from playing the role of the plants of this habit in the lowland forests. *Marcgravia brownei* is by far the largest and most striking of the climbers, growing into the canopy of the forest, filling the crowns of the largest trees, and hanging in graceful festoons from their lower limbs. Its juvenile shoots are commonly seen growing closely appressed to smooth naked trunks, their small deltoid leaves forming a striking contrast to the long pinnate leaves of the adult shoots. *Anthurium scandens* is the only climbing aroid; its small simple leaves give it a far less important place in the physiognomy of the vegetation than is held by the species of *Anthurium* and *Philodendron* of the lowlands. Other frequent lianes are *Smilax celastroides*, *Blakea trinervis*, *Mctastelma fawcettii*, *Metastelma atrorubens*, *Bidens shrevei*, and *Begonia scandens*. Among the ferns *Blechnum attenuatum* and *Polypodium loriceum* are common in ravines and slopes alike, but seldom climb far above mid-height in the forest. The climbing filmy-ferns, *Trichomanes radicans* and *Trichomanes scandens*, are confined to deep shade in the narrowest ravines and seldom reach over 6 feet from the ground.

Plate 10

Mid-level aspect of tall forest in a shallow Windward Ravine. In the middle at left, the epiphytic *Columnea hirsuta;* above and below it, the climbing *Polypodium loriceam.* Above the tree-fern is *Bochmeria caudata,* to its left *Guarea swartzii,* to its right *Meeranium purpurascens.* The large trees are *Solanum punctulatum.*

WINDWARD SLOPES.

On emerging from a ravine and climbing onto its slopes a number of notable changes in the vegetation are encountered at once; the stature of the forest is much less, varying from 30 to 50 feet (9 to 15 meters), and its canopy is much more open. The trees exhibit a striking diversity in trunk diameter, and all but the youngest have a down-hill inclination which brings many of the oldest into a nearly horizontal position. The leaning trees and downfallen trunks bring the epiphytic vegetation into the lower layers of the forest, and not infrequently colonies of bromeliads and epiphytic orchids may be found on the ground, rooted on the rotting remains of the trunk with which they fell. A more dense undergrowth and a more sparse herbaceous terrestrial vegetation characterize the slopes in comparison with the ravines, and the number of Pteridophytes is also much less, the climbing and epiphytic species being more observable, by reason of here occupying a place nearer the floor of the forest. The hanging mosses are absent, and the tree-ferns less frequent, at the same time that the thicket-forming ferns begin to be encountered.

The Windward Slopes vary in their character, according as they are nearer the bottom of a valley or nearer a ridge, and indeed the vegetation of the slopes is little more than a mean between the pronouncedly hygrophilous ravines and the open sub-alpine ridges. The slopes which lie just below gaps are similar to ravines, as may be noted to the north of Portland Gap and New Haven Gap, depressions in the main ridge through which clouds are rolling almost continuously.

The forest of the Windward Slopes is made up predominantly of *Clethra occidentalis, Podocarpus urbanii, Vaccinium meridionale, Cyrilla racemiflora, Ilex montana* var. *occidentalis, Alchornea latifolia,* and *Brunellia comocladifolia.* These vary from place to place in their relative abundance, but their order as above given is approximately that of their frequency of occurrence. With them and much less frequent are *Hedyosmum arborescens, Clusia havetioides, Nectandra patens, Hæmocharis hæmatoxylon, Rhamnus sphærospermus, Eugenia marchiana, Rapanea ferruginea, Weinmannia pinnata,* and *Cleyera theoides.* A few under-trees and shrubs that are particularly common are *Mecranium purpurascens, Tamonea rubens, Tournefortia cymosa, Palicourea crocae, Acalypha virgata, Hæmocharis villosa, Lisianthus latifolius,* and the tree-ferns *Cyathea furfuracea, Cyathea insignis,* and the large-leaved but acaulescent *Alsophila quadripinnata.*

The distinctly terrestrial herbaceous plants of the slopes are few as compared with the downfallen epiphytes, comprising conspicuously *Pteris longifolia, Blechnum capense, Polystichum denticulatum,* the broad-leaved grass *Olyria latifolia,* the sedges *Rynchospora eggersiana* and *Uncinia hamata,* together with *Pilea parietaria, Lobelia assurgens, Peperomia basellæfolia,* and *Lycopodium reflexum.* Among the downfallen

epiphytes, by far the most common are species of *Elaphoglossum*—*Elaphoglossum latifolium*, *Elaphoglossum inæqualifolium*, and *Elaphoglossum petiolatum*—together with the orchid *Stelis ophioglossoides*, species of *Dichæa*, and the common bromeliad *Caraguata sintenesii*. Throughout the forest *Chusquea abietifolia* forms thickets or climbs over the lower trees, often making passage through the forest difficult; the only other common lianes are *Manettia lygistum*, *Cionosicys pomiformis*, and *Smilax celastroides*.

LEEWARD RAVINES.

The ravines of the leeward slopes of the Blue Mountains differ strikingly from those of the windward side, exhibiting few of the most pronounced characteristics of rain-forest. The general structure of the two types is similar, both in the stature of their trees and in the irregular canopy which gives place to abundant under-trees and shrubs. Many of the same species of trees occur in the ravines of the two sides of the range, and many of the epiphytes, but few of the terrestrial herbaceous plants. The most striking difference between the two ravine types is in the absence from those of the leeward side of garlands of hanging moss and the beds of epiphytic mosses and hepatics, the much scanter growth of epiphytes in general, together with the scarcity of tree-ferns, the inconspicuousness of filmy ferns, and the predominance of herbaceous vegetation made up of a small number of fern species of a less hygrophilous character and a number of flowering plants. The leeward side of the range receives a lighter rainfall, has much less fog, and a reciprocally increased number of hours of sunshine, factors which combine to lower the atmospheric humidity and increase the insolation to a degree that modifies fundamentally the life conditions and makes the habitat an unfavorable one for very many of the species so common in the Windward Ravines, at the same time that they bring into the vegetation a number of trees, shrubs, epiphytes, and other plants, the range of which extends down to 3,000 and 2,000 feet (915 meters and 610 meters), but does not cross the main ridge onto the Windward Slopes. By far the largest number of these middle-altitude forms are absent from the Leeward Ravines and find their optimal conditions in the still drier Leeward Slopes, on which the climate is nearer that of the lower altitudes.

The commonest trees of this habitat are *Gilibertia arborea*, *Alchornea latifolia*, *Ilex montana* var. *occidentalis*, *Brunellia comocladifolia*, *Psychotaria brownei*, and *Psychotaria corymbosa*. The commonest under-trees are *Bœhmeria caudata*, *Datura suaveolens*, *Phenax hirtus*, *Acnistus arborescens*, *Piper geniculatum*, and *Malvaviscus arboreus*. The herbaceous vegetation is dominated by *Pilea grandifolia* and an assemblage of species of *Asplenium* and *Dryopteris*—notably *Asplenium pteropus*, *Asplenium lunulatum* var. *strictum*, *Asplenium obtusifolium*, *Asplenium*

A. The commonest herbaceous plant of the Ravines: *Pilea nigrescens*, above and below it *Deplazium celtidifolium*.

B. Two extremely hygrophilous plants: *Peperomia hispidula* (round leaves at center) and *Peperomia filiformis* (elliptical leaves below).

Characteristic interior of Windward Slope Forest, showing inclination of trunks due to erosion. At the lower right is *Polystichum denticulatum*, at the left the epiphytic *Polypodium suspensum*. Above the *Polystichum* is a young *Podocarpus*, and a colony of *Elaphoglossum inaequalifolium*.

Interior of a Leeward Ravine at 4,500 feet. The central tree is *Alchornea latifolia*, the shrubs in the background are *Bahmeria*, the herbaceous plants *Pilea grandifolia*.

A. Looking over Leeward Slopes and ruinate in the vicinity of Cinchona. The isolated dark trees are *Juniperus barbadensis*.

B. Bridle path through Leeward Slope Forest, with overhanging masses of the climbing bamboo, *Chusquea abietifolia*.

cristatum, and *Dryopteris effusa*, *Dryopteris patens*, *Dryopteris ampla*, and other species for which it has not been possible to secure determinations. *Peperomia turfosa*, *Pilea parietaria*, *Rynchospora eggersiana*, *Calanthe mexicana*, *Spiranthes* sp., and several other orchids are infrequent in occurrence.

LEEWARD SLOPES.

Both the climatic conditions and the vegetation of the Leeward Slopes differ considerably between the lowest altitudes which are being considered and the upper slopes in the vicinity of the main ridge of the Blue Mountains. The latter resemble in many respects the ridges, to be described presently, and differ from the former not so much by reason of their difference in altitude as on account of the greater rainfall at the higher slopes and the fact that they are enveloped in fog during a good share of the time that the lower slopes are in sunlight. What is to be said of the Leeward Slopes accordingly relates to the lower altitudes, while the higher ones—that is to say those within 500 vertical feet (153 meters) of the main ridge—are comprised in the ridge type of forest.

The Leeward Slopes depart still more than the Leeward Ravines from the typical rain-forest which has been described. An arborescent flora richer than that of the Windward Ravines and Slopes forms a forest of low stature, in which individuals of large and small trunk diameter are intermingled to form a closed canopy. There is little distinction between the crowns of the largest trees and the foliage of the smaller trees and shrubs, so that there is frequently a solid mass of foliage from the canopy to the ground. The hygrophilous mosses and hepatics are scarce, and the epiphytic vegetation is scant and confined to the more xerophilous forms of the ridge forest. Lianes are abundant, as are also a number of loranthaceous parasites. The terrestrial herbaceous species are largely phanerogamic, while the pteridophytic ones include a large number of species of ferns represented by infrequent individuals, and a small number of lycopodiums which are extremely abundant.

The trees of the Leeward Slopes are in part species which also occur on the slopes of the windward side, together with others which range upward from far below our area. The most common are: *Clethra occidentalis*, *Vaccinium meridionale*, *Ilex montana* var. *occidentalis*, *Alchornea latifolia*, *Brunellia comocladifolia*, *Rapanea ferruginea*, *Cyrilla racemiflora*, *Juniperus barbadensis*, *Cleyera theoides*, *Lyonia jamaicensis*, *Citharexylum caudatum*, *Viburnum villosum*, *Viburnum alpinum*, *Eugenia harrisii*, *Dipholis montana*, *Daphnopsis tinifolia*, *Gilibertia arborea*, *Cestrum* sp., *Heterotrichum patens*, *Psidium montanum*, and *Tamonea rubens*. A large number of smaller trees and shrubs are characteristic of these slopes, some of them dominating the areas of ruinate which are

returning to forest. Commonest of these are: *Bachharis scoparia* and *Dodonæa angustifolia;* others are *Garrya fadyenii, Acalypha virgata, Oreopanax capitatum, Bocconia frutescens, Myrica microcarpa, Malvaviscus arboreus, Eupatorium parviflorum, Micromeria obovata, Hedyosmum nutans,* and *Vernonia intonsa.*

The herbaceous vegetation, although rich in species, is not so rich in individuals as the most luxuriant spots in the Windward Slopes, and is characterized by the entire absence of all the most hygrophilous species of the northern side of the range. Thickets of *Gleichenia pectinata* and *Odontosorea aculeata* are frequently encountered, particularly at the higher altitudes, and beneath them the ground is bare of vegetation and very densely shaded. *Pteridium aquilinum* also frequently forms thickets, but they are much more open and accompanied by sedges and grasses.

In the more heavily wooded portions of the Leeward Slopes the commonest herbaceous plants are *Pilea grandifolia, Uncinia hamata, Rynchospora eggersiana,* and *Rynchospora polyphylla.* On steep banks and shaded rocks may be found *Pilea microphylla, Pilea parietaria, Peperomia turfosa, Peperomia rupigaudens, Vittaria lineata,* and *Antrophyum lineatum.* In more open situations *Lycopodium clavatum, Lycopodium cernuum,* and *Lycopodium fawcettii* form such extensive growths as to be very conspicuous. *Begonia nitida* and *Begonia acuminata* are frequent on steep slopes, and the orchids *Epidendrum cochleatum, Epidendrum ramosum,* and *Epidendrum verrucosum.* The commonest ferns are *Polystichum struthionis, Dryopteris effusa, Blechnum capense, Nephrolepis cordifolia, Blechnum occidentale,* and *Pteris longifolia,* to which might be added over one hundred that occur sporadically. Other plants of interest which give character to this habitat are *Rubus alpinus, Iresine celosioides, Lobelia caudata, Ascyrum hypericoides, Liabum umbellatum, Spiranthes elata, Polypodium crassifolium,* and *Lantana camara.*

The number of species of lianes is greater in these forests and the ruinate than it is on the Windward Slopes, but they are no more conspicuous as an element of the vegetation. They comprise commonly: *Smilax celastroides, Passiflora sexflora, Passiflora penduliflora, Metastelma atrorubens, Metastelma ephedroides, Ipomœa triloba, Manettia lygistum,* and the herbaceous woolly-leaved *Relbunium hypocarpium.* The loranthaceous parasites are also conspicuous, including *Loranthus parvifolius, Phoradendron flavens, Dendrophthora cupressoides,* and *Dentrophthora gracilis.*

The outcroppings of limestone scattered over the Leeward Slopes usually project above the shade of the forest and are occasionally large enough to support small trees of *Juniperus barbadensis,* bushes of *Baccharis scoparia* and *Micromeria obovata.* In their crevices and pockets occur a number of plants, some of which are not found else-

Interior of Ridge Forest at 5,000 feet. The trees are *Clusia hartioides* (on the right), *Cyrilla racemiflora*, *Vaccinium meridionale*, and *Rapanea ferruginea*. The undergrowth is chiefly *Gleichenia pectinata*.

where in the region, others of which are epiphytes at lower altitudes, as: *Peperomia verticillata, Tillandsia complanata, Isochilus linearis, Bryophyllum calycinum, Epidendrum verrucosum, Polypodium incanum, Polypodium lanceolatum, Polypodium plumula, Cheilanthes microphylla,* and *Asplenium dimidiatum.*

THE RIDGES.

The Ridge Forest of the Blue Mountains is stunted, open, and relatively xerophilous in the entire make-up of its vegetation. It possesses few of the species characteristic of ravines, at the same time that a distinct set of characteristics are the salient ones in determining its physiognomy. The main ridge of the Blue Mountains at 5,600 to 6,000 feet altitude exhibits the most marked type of Ridge Forest, excepting at the low gaps. Radiating from the main ridge along the principal lateral ridges and from them in turn along the lesser water-partings extend the narrow stretches of Ridge Forest, retaining much the same character down to 4,500 feet and differing only in minor particulars on the windward and leeward sides of the range. On leaving any part of the Ridge Forest and descending to a distance of 100 feet the characteristics of the slopes will be found to prevail.

The Ridge Forest presents a very level canopy when viewed at a distance, but it varies greatly in the density or openness of its stand of trees. In the most dense stands, however, the trees are sufficiently far apart for their crowns not to meet, which fact, together with the sparsity and openness of the shrubby vegetation, allows considerable light to reach the forest floor. The trees vary from 18 to 30 feet in height, but are of incommensurate trunk diameter, often making 2 and 3 feet in thickness with a height of 16 to 20 feet. The largest trunks are bent and gnarled or prostrate on the ground, and so interlocked with dead and decaying trunks that the forest floor is seldom clear for a space as much as 15 feet square (see plate 17).

The under-trees are scant, but young individuals of the principal tree species are common, as are also xerophilous shrubs, chiefly occurring in the most open parts of the forest. The more open the forest the more completely is it occupied by the bamboo, which literally fills the forest from the ground to a height of 6 or 8 feet; or in other open places the bamboo is absent and dense thickets of ferns cover the ground to a depth of 4 or 5 feet, excluding all smaller vegetation. Only in the portions of the Ridge Forest with a closed canopy is the floor clear enough to give space to a small number of herbaceous species, which are chiefly ferns and the sedges *Rynchospora polyphylla* and *Rynchospora elongata.*

The epiphytic vegetation is not conspicuous, indeed hardly as much so as are the parasitic Loranthaceæ, although actually embracing a considerable number of species. These are mostly bromeliads and small species of *Polypodium* and *Liparis,* while mosses, the hepatic

Herberta, lichens, and blue-green algæ form a considerable portion of the epiphytic growth on the slender limbs of the largest trees. On the prostrate trunks and lower limbs are thick mats of mosses and hepatics, or colonies of Hymenophyllaceæ, in which often grow larger ferns, orchids, and lycopods.

The few moist depressions alluded to as occurring on the main ridge are filled with *Sphagnum lesucurii* and *Rynchospora polyphylla*, but are not without trees growing in their midst and have no species which are peculiar to them. *Sphagnum* is common elsewhere in the Blue Mountains, both on the ground and growing as an epiphyte, while on the summit of Guava Ridge, in the Port Royal Mountains, is an open bog, filled with sphagnum and having a close resemblance to North Temperate peat bogs.

The commonest trees of the Ridge Forest, together forming perhaps one-fourth of the stand, are *Podocarpus urbanii* and *Clethra alexandri:* very abundant are: *Vaccinium meridionale*, *Rapanea ferruginea*, *Weinmannia pinnata*, *Cyrilla racemiflora*, *Myrica microcarpa*, *Ilex montana* var. *occidentalis*, and *Eugenia alpina*. Less frequent are: *Cleyera theoides*, *Eugenia lateriflora*, *Clusia havetioides*, and *Rhamnus sphærospermus*. The degree to which many of the above species are present only as stunted individuals of 4 to 8 feet in height is indicated in plate 19 and plate 20. *Ilex obcordata* is a common shrub sometimes attaining to the height of a tree and, with *Eugenia alpina*, exhibiting the smallest leaves of any trees in the region (see plate 20 A). A form of *Palicourea crocea* is common, together with *Miconia rigida*, *Wallenia crassifolia*, and *Lisianthus latifolius*. The Compositæ contribute several shrubs to the ridge vegetation, notably *Vernonia divaricata*, which forms extensive thickets in open stands of forest, particularly on the main ridge between Sir John and Mossman's Peaks, *Eupatorium dalea*, *Vernonia arborescens*, *Senecio fadyenii*, and *Eupatorium critoniforme*. One of the most striking plants of the ridges is *Lobelia martagon*, which has a woody stem branched once, growing to a height of 7 feet and bearing tufts of leaves at the ends of its branches, with its spikes of dark-red flowers. The exposure of the ridges to high wind is probably accountable for the absence of tree-ferns, as just below the most exposed of the ridges, in forest of similar character, may be found *Cyathea furfuracea* and *Cyathea insignis*.

The thickets of ferns are made up chiefly of *Gleichenia jamaicensis*, *Gleichenia bancroftii*, and *Odontosorea aculeata*, but are frequently also formed by *Pteridium aquilinum*, *Histiopteris incisa*, *Pteris deflexa*, and *Hypolepis nigrescens*. Within the denser forest the open floor is most conspicuously covered with *Rynchospora polyphylla* and *Blechnum capense*, in addition to which *Peperomia basellæfolia*, *Pteris longifolia*, and *Plagiogyria biserrata* occur, together with downfallen epiphytes and the seedlings and suckers of the trees.

Looking over the canopy of Ridge type of rain-forest in the vicinity of New Haven Gap at 5,700 feet. In the foreground, *Clethra occidentalis* (left) and *Rapanea guianensis* (right). Fog is seen rising from the Mabess Valley.

THE PEAKS.

An examination of Blue Mountain Peak and Sir John Peak showed them to be essentially identical in their vegetation in spite of their difference of 1,200 feet in altitude. In flora the peaks perhaps differ somewhat more from the lower parts of the range than they do in their vegetation. Several species have been described which are supposed to be confined to the summit of Blue Mountain Peak or to its higher slopes, but so little is known of the regions immediately surrounding the peak and off the single bridle road by which the summit is accessible that these species may be turned up elsewhere. Indeed, the peak possesses no more endemic forms than do many other areas of the same size in the island. That many of the mountain species are absent from Blue Mountain Peak is altogether likely, although no one has ever made a sufficiently thorough examination of the locality to be warranted in stating what these species are.

The vegetation of the Peaks exhibits a mere accentuation of the characteristics that have been described for the Ridges—the forest is low and extremely open, the tallest trees seldom exceeding 20 feet, with under-sized individuals of the dominant trees and various shrubs forming the bulk of the stand, thickets of *Gleichenia* and *Pteridium* occupying the open places. The essential similarity of the vegetation to that of the Ridges is due to the high winds to which the two habitats are alike subjected and to the possible fall of soil-moisture content previously alluded to.

The characteristic trees of the summit of Blue Mountain Peak are *Clethra alexandri*, *Podocarpus urbanii*, *Gilibertia nutans*, *Vaccinium meridionale*, *Ilex montana* var. *occidentalis*, and *Eugenia alpina*. Less frequent, and usually occurring as shrubs, are: *Ilex obcordata*, *Cleyera theoides*, *Weinmannia pinnata*, *Viburnum villosum*, and *Rhamnus sphaerospermus*. A striking under-tree, apparently confined in occurrence to the summit of Blue Mountain Peak, is *Senecio laciniatus*, which has a soft, woody stem, large leaves, and very conspicuous yellow flowers. In addition to it all of the composite shrubs mentioned as occurring on the Ridges are important components of the scrub which covers the highest peaks. In addition to the thicket-forming ferns, *Gleichenia jamaicensis* and *Odontosorea aculeata*, common throughout the highest parts of the Ridge forest, *Pæsia viscosa*, *Hypolepis pulcherrima*, and *Hypolepis repens* are common at the highest altitudes. Almost equally conspicuous with the fern thickets are the beds of *Lycopodium*, sometimes 20 to 40 feet in diameter, and made up of *Lycopodium clavatum*, *Lycopodium fawcettii*, and *Lycopodium cernuum*. In the absence of fern or lycopod thickets, *Blechnum capense* and *Rynchospora pallida* are the characteristic inhabitants of the forest floor, while in more deeply shaded situations *Asplenium lunulatum* and *Pilea parietaria* var. *alpestris* are common. With the exception of the bromeliads

Tillandsia incurva and *Caraguata sintenesii*, the epiphytic plants at the high peaks are exclusively small orchids and ferns, polster-forming mosses, xerophilous hepatics, lichens, and Cyanophyceæ.

The summit of John Crow Peak reaches nearly the altitude of Sir John Peak, but is strikingly different from it in its vegetation, owing to its summit being part of a limestone dyke running southeast into the valley of the Clyde River. The bare rock of the summit is eroded into a honeycombed surface with knife-like edges and pockets of soil, in which is supported a stunted and open forest. *Cyrilla racemiflora*, *Rhamnus sphærospermus*, and *Eugenia fragrans* are here quite common, to the exclusion of the familiar species of the other peaks. *Fagara hartii*, *Brunfelsia harrisii*, *Eugenia marchiana*, *Acalypha virgata*, *Gymnanthes elliptica*, *Chœnocephalus* sp., and *Eupatorium critoniforme* are all either peculiar to this peak or characteristic in its vegetation. Drought-resistant shrubs with prodigious thickets of *Chusquea* dominate the upper slopes of John Crow Peak to the almost total exclusion of all the forms characterizing the rain-forest by which it is surrounded.

EPIPHYTES.

The epiphytic plants occupy quite as conspicuous a place in the total assemblage of vegetation in the Montane Rain-forests as they do in any of the lowland plant formations of Jamaica. At the lower altitudes to windward of the Blue Mountains the lofty forest is relatively poor in epiphytes excepting in the tops of the trees, where Bromeliaceæ and Orchidaceæ are the commonest forms. In the savannas of the southern coast and in the central part of the island the species of *Tillandsia* are by far the most prominent epiphytes, with which are usually found a number of Orchidaceæ and the single species of *Bromelia* present in the island. In the rain-forest of the mountains every type of epiphytic plant is represented, the bromeliads, the orchids, a number of woody forms, ferns of every description from the most delicate Hymenophyllaceæ to extremely small drought-resistant polypodiums, flowering plants, both hygrophilous and succulent, as well as mosses, hepatics, and lichens.

Schimper[1] pointed out the differences between the epiphytic vegetation of the forest floor and the canopy, and I have shown in a previous paper[2] that a similar difference exists in the case of the Hymenophyllaceæ and that it is determined by the vertical difference between the climate of the floor of the forest and its canopy, a factor which is operative in the case of all the epiphytic vegetation. The contrast between the epiphytes of the lowest level of the forest and the tree-tops is greater than in the lowland forests, due, of course, to the

[1]Schimper, A. F. W. Die Epiphytische Vegetation Amerikas. Bot. Mitth. aus den Trop., Heft I, 1888.

[2]Shreve, F. Studies on Jamaican Hymenophyllaceæ. Bot. Gaz. 51 : 184-209. Mar., 1911.

Interior of Ridge Forest at 5,900 feet on the main ridge of the Blue Mountains. The large trunks are chiefly *Vaccinium* and *Podocarpus*.

Interior of forest on summit of Sir John Peak, at 6,200 feet. The large trees are *Podocarpus urbanii*, on the right is a branch of *Cleyera theoides*. The undergrowth is *Gleichenia jamaicensis* and *Blechnum capense*. On the limbs are mats of the hepatic *Herberta*.

Vegetation of most exposed Ridges at higher altitudes, with edge of relict alpine meadow; slopes of Sir John Peak at 6,100 feet. The tree is *Clethra alexandri*, the grass *Danthonia shrevei*.

Vegetation of the main ridge east of Sir John Peak. On the sky line are *Podocarpus urbanii* and *Eugenia alpina*, in the foreground *Clethra alexandri* and *Gleichenia jamaicensis*.

higher and more constant humidity at the floor in the mountain forests. The epiphytes of the lowest level are pronounced hygrophytes, confined to that level by its favoring conditions of humidity and frequent wetness. The mid-level forms are somewhat drought-resistant or else confined to the proximity of water-storing mats of bryophytes, or they may have a water-storing tissue. The epiphytes of the topmost level are pronouncedly xerophilous, with either water-storing or water-catching structures, or else they are small and coriaceous.

The Windward Ravines exceed by far all of the other mountain habitats in the wealth of their epiphytes, because in them can be found not only their own peculiar forms, but in the tops of the tallest trees are to be found the forms characteristic of the Ridge Forests, while at mid-height in the Ravines are to be found those characteristic of the Slopes.

The commonest terrestrial ferns, orchids, and species of *Pilea* are not very commonly found as epiphytes, even at the lowest level in the forest, but the succulent Peperomias—*Peperomia basselæfolia* and *Peperomia filiformis*—with the non-succulent *Peperomia hispidula*, are low epiphytes, growing with *Trichomanes capillaceum, Trichomanes hookeri, Trichomanes pyxidiferum*, and *Hymenophyllum fucoides*. Such filmy ferns as *Hymenophyllum asplenioides, Hymenophyllum tunbrigense, Hymenophyllum crispum*, and *Hymenophyllum polyanthos* grow frequently on rather bare trunks, as do also *Polypodium suspensum* and *Polypodium cultratum*, forms distinguishable by their pendant fronds. In the case of the majority of forms, however, which occur more than a few feet above the ground, the existence of a moss substratum is essential to their occurrence. The more resistant filmy-ferns, *Hymenophyllum polyanthos, Hymenophyllum crispum*, and *Hymenophyllum fucoides*, are very common at middle elevations in the forest, growing in beds of liverworts, beneath which such pendant forms as *Hymenophyllum sericeum, Hymenophyllum axillare, Elaphoglossum squamosum*, and *Elaphoglossum villosum* are common in occurrence.

The largest of the epiphytes is *Sciadophyllum brownei*, an araliaceous plant sometimes growing independently, sometimes a half-climber, but more frequently epiphytic at mid-level in company with the gesneraceous *Columnea hirsuta* and the melastomaceous *Blakea trinervis*—also often rooted in the soil. Seedlings of *Clusia havetioides* are also frequent as epiphytes, seedlings of other trees being rare off the ground. *Peperomia obtusifolia* var. is conspicuously frequent, as are also some of the numerous species of *Elaphoglossum* (*Elaphoglossum latifolium, Elaphoglossum inæqualifolium*, and *Elaphoglossum pallidum*) and the striking *Lycopodium taxifolium*. The larger epiphytic orchids are very numerous, although there are but few species of them. *Stelis ophioglossoides* and *Dichæa graminea* are forms with water-storing leaves and thin roots, while *Dichæa glauca* has thin leaves and stout roots with

well-developed velamen. *Epidendrum verrucosum* has water-storing leaves and false bulbs, and *Liparis clata* has water-storing false bulbs and thin leaves, and seldom emerges far from the forest floor.

In the highest level of the tree-tops the epiphytes are small plants in every case excepting the common tank-epiphyte, *Caraguata sintenesii*, which also grows in the mid-levels. The small orchids of the tree-tops are all provided with water-storing tissue in their leaves, commonest among them being *Lepanthes concinna*, *Lepanthes tridentata*, *Lepanthes concolor*, and *Pleurothallis* sp. The small ferns growing with these orchids are mostly species of *Polypodium*—*Polypodium gramineum*, *Polypodium marginellum*, and *Polypodium serrulatum* being common. A large white *Usnea* and a smaller yellow species, together with the basidiomycetous lichen *Cora pavonia*, are common in the tree-tops, particularly on the Ridges at higher elevations, where they grow with the polster mosses *Macromitrium* and *Sclotheimia*.

To proceed from a Windward Ravine up through Slope forest to a Ridge would bring to view in the lower levels of the forest the same transition in epiphytic vegetation that might be seen by climbing a tall tree in a ravine, except that lichens are not conspicuous in the canopy of the Ravines, and the mid-height epiphytes are often found in favorable spots on the ridges. The importance of a living water-conserving substratum for the occurrence of the mid-height epiphytes is everywhere apparent on the slopes and ridges.

I have shown in an earlier paper[1] something of the comparative power of drought resistance in *Stelis ophioglossoides*, a typical leaf-storage epiphyte, and *Caraguata sintenesii* a typical tank-epiphyte (incorrectly designated as *Guzmania tricolor* in the paper alluded to). When deprived of its catch of water *Caraguata* exceeded *Stelis* in its ability to persist in the absence of renewed supplies of water while kept in the laboratory for fifty days. During the longest periods of drought to which these forms are apt to be subjected *Caraguata* would be exposed to conditions more favorable to water-loss than would *Stelis* in its mid-height position in the forest, so it is probable that under natural conditions the two types would both meet the limit of their resistance at the end of six or seven weeks without renewed supplies of water, an extreme condition which the weather records would indicate has happened but once in the past thirty-nine years, this occasion being in the vicinity of New Haven Gap in the spring of 1892 (see p. 15).

With such capacity for drought resistance may be contrasted the character of the most hygrophilous of the filmy-ferns, such as *Trichomanes capillaceum* and *Trichomanes rigidum*, to which the total deprivation of water for seventy-two hours is fatal, provided the surfaces of the leaves are dried off at the outset of the period and the humidity

[1] Shreve, F. Transpiration and Water Storage in *Stelis ophioglossoides*. Plant World, 11: 165-172, Aug. 1908.

An epiphytic colony of the drought-resistant filmy fern *Hymenophyllum sericeum*, growing with *Cladonia* sp., *Stelis ophioglossoides*, and *Caragnata sintenesii*.

is playing through its usual range in the vicinity of Cinchona (see plate 22). That other species of the Hymenophyllaceæ have acquired semi-xerophilous characteristics which enable them to persist in the mid-levels of the forest in company with *Caraguata* (see plate 22) and to endure the same conditions to which it is liable, is one of the most striking features of the rain-forest.

THE RELATION OF PHYSICAL CONDITIONS TO HABITAT DISTINCTIONS IN THE RAIN-FOREST.

During my visit to the Blue Mountains in the winter of 1905–06 I carried on instrumentation designed to give some evidence as to the degree and manner in which the climatic conditions within the rain-forest depart from the normal conditions of the open slopes at Cinchona on which the longer series of data was secured which have already been presented; and also to determine what some of the differences of conditions are that may be responsible for the distinctions in the vegetation of the habitats that have been described.

It requires but a casual visit to the region to realize that the most salient characteristics of the vegetation are determined by the high rainfall—unbroken by a pronounced dry season—together with the high percentage of cloudiness and fog, with all the subsidiary conditions of moist soil, moist atmosphere, small percentage of insolation, wetness of foliage and the like, which follow in their train. Furthermore the moisture conditions are the most important set of differential factors in determining the diverseness of the several habitats.

Rainfall readings are almost meaningless for a region in which, as here, ten showers of two hours' duration each may give only a total fall of 1 to 2 inches, whereas on another day a single fall of two hours' duration may give the same amount, with a totally incommensurate effect on the other moisture conditions and on the vegetation. Furthermore, a light rain followed by several days of continuous fog will have a very different significance from a heavier fall followed by two or three hours of insolation. The irregularity of the rainfall (see p. 15) together with the fact that the moistness of the atmosphere, the wetness of the foliage, and to an extent even the moistness of the soil, are due as much to fog as to actual precipitation of drops large enough to be called rain, gives the rainfall figures only the most general bearing on the conditions present. So well distributed is the rainfall, so low the evaporating power of the air, and so unbroken the vegetational covering, that the state of moistness of the soil is a factor which can be safely neglected throughout periods of normal weather. I have already called attention to the occasional periods of very light rainfall, during which it is possible for the soil moisture of the ridges and peaks to fall to an extent that would make this factor one of importance. I had an opportunity

in 1903 to observe the effects of a prolonged season of dryness, but the chance to secure soil-moisture determinations for such a period has not recurred since I have been interested in the subject.

My instrumentation has, accordingly, centered in the determination of the atmospheric moisture conditions, extending also to the securing of air and soil-temperature readings. Automatic traces of the daily play of the humidity conditions were secured by use of a hygrograph, which was combined with a thermograph in the type of double register made by Friez. Owing to the practical exigencies of the work, only one of the instruments was used, which was moved from place to place to secure the several records, thereby making it impossible for me to obtain simultaneous readings from different stations. The general uniformity of the weather conditions through the winter of 1905–06 kept this circumstance from seriously impairing the comparableness of the various record slips. The instrument was installed about 3 feet from the ground, on a portable framework of boards, and protected by a white water-proofed canvas placed so as to be at least 1 foot from the instrument above and at the sides, while the ends, together with the open base, gave a free access of air. A soil thermograph of the Hallock type, made by Friez, was also used, being usually installed with the double register or else in a similar manner. The cylinder was buried at a depth of 1 foot in all cases; a hole was dug, from which a tunnel was made to one side for the cylinder, and the earth was packed in naturally. In this manner the soil above the cylinder was left undisturbed.

The hydrograph was corrected at the beginning and end of each week in accordance with sling-psychrometer readings. The thermograph was also verified in its reading twice for each sheet; the soil thermograph three times for the period of five months over which it was used. The thermograph and hygrograph traces presented in the accompanying plates have been redrawn from the originals. This has lost them something of their detail, but has been necessary to the incorporating of the corrections, as well as to the manner of their reproduction.

During the summer of 1909 a number of readings were taken at Cinchona and in the rain-forest with the type of atmometer devised by Livingston.[1] The atmometers were protected from rain by suspending a small pane of glass horizontally at a few inches above the tip of the cup. The error due to the wetting and impact of rainfall in the ordinary atmometer when not covered by glass is considerable, and is most satisfactorily obviated by the use of the rain-correcting type of instrument more recently invented by Livingston.[2] Readings with an instru-

[1]Livingston, B. E. The Relation of Desert Plants to Soil Moisture and to Evaporation. Carnegie Inst. Wash. Pub. 50, 1906. Also: Operation of the Porous Cup Atmometer. Plant World, 13 : 111–119, 1910.

[2]Livingston, B. E. A Rain-correcting Atmometer for Ecological Instrumentation. Plant World, 13 : 79–82, 1910.

A. Shoots of *Ilex obcordata* (left) and *Eugenia alpina*, the smallest-leaved trees of the highest peaks.

B. Series of potted plants as used in transpiration experiments. From left to right: *Pilea nigrescens*, *Peperomia turfosa*, *Peperomia basellæfolia*, *Diplazium celtidifolium*, *Asplenium alatum*, and porous cup atmometer mounted for weighing.

ment of this type were taken by Brown[1] at my Windward Ravine station in the summer of 1910, extending through four weeks.

In the still air of the floor of the rain-forest, where the temperature ranges through less than 10° a day, the atmometer is in effect a hygrometer, registering the cumulative evaporation of the longer intervals when the humidity falls below the prevalent high percentages. The ratio of the rate of evaporation from a free water surface to that from a standard cup has been found to be 0.76 at Cinchona as compared with 1.15 at Tucson. This points to a difference in the character of the evaporating water film under the two diverse climates, the film probably being discontinuous in the drier climate, occupying only the pores of the cup, while it is continuous in the moist climate, occupying the entire surface. The difference between the dry look of the surface of cups in operation at Tucson and their moist look when in operation at Cinchona corroborates this explanation. The existence of a greater surface film would have the effect of increasing the evaporating surface of the cup, and would accordingly lower its ratio to a free water surface as compared with this ratio determined in an arid climate. While these considerations make it necessary to apply a considerable correction to atmometer readings from widely diverse climates before comparing them, they do not at all invalidate the comparableness of readings taken under similar humidity conditions. In rain-forest ravines the atmometer is subject to the condensation of moisture onto its evaporating surface, whenever evaporation cools this a few degrees below the air temperature. The condensation stops evaporation and cooling, and permits the surface of the cup to warm up again and presently to resume evaporation. The low rates of evaporation obtainable with the atmometer in Windward Ravines are undoubtedly somewhat lower than they should be for this reason.

After repeated observations with the hygrograph and sling psychrometer, I am convinced that saturation, or even humidities as high as 97 to 99 per cent, are extremely transitory states of the atmosphere in the most moist situations in the rain-forest. Saturation must precede precipitation; and the condensation of moisture on the foliage of plants often takes place in the deep forest. As soon as precipitation or condensation occurs, there is a fall in the humidity and it naturally rises again but slowly, for although the extent of wet surfaces capable of adding by evaporation to the moisture of the air is very great, the high humidity itself retards such evaporation. Cloudiness is an important factor in influencing humidity as well as is fog. The passage of small clouds over the face of the sun causes immediate and pronounced rises in humidity, due in great measure to the sudden fall of temperature which may be too transitory to affect the sluggish thermograph.

[1]Brown, W. H. Evaporation and Plant Habitats in Jamaica. Plant World, 13 : 268–272, 1910.

HUMIDITY.

I am not able to give any figures or records to show satisfactorily what differences there may be between the moisture conditions at different altitudes on the Windward Slopes of the Blue Mountain Range. The rainfall of 130 inches at Port Antonio is due to heavy showers which are often confined to the vicinity of the coast. Localities off the coast at 1,000 to 3,000 feet altitude receive less than that amount of rain. The upper zone of heavy rainfall begins at about 4,000 feet, and extends to the summit of Blue Mountain Peak. The fact that the fall for New Haven Gap is 113 inches and that for Blue Mountain Peak 168 inches indicates that the fall increases steadily with increase of altitude. Even more important than the rainfall conditions is the behavior of the cloud mass which is so characteristic of the windward slope. Judging from my repeated visits to the windward side of the range, from one to three times a week at all seasons of the year, I may hazard the estimate that during February, July, and August these slopes are enveloped in cloud for 30 per cent of the daylight hours, and during the other months of the year for 70 per cent of them. The nights are always clear, and it not infrequently happens in the winter months that lower humidities occur at night than those prevalent during the day. Several times I have watched the sunrise from Blue Mountain Peak or from the Main Ridge in the vicinity of Sir John Peak, and have noticed that it was only 5 to 15 minutes thereafter when clouds began to form. An hour to two hours after sunrise there would be a solid cloud blanket over the entire north slope. Detached fragments from this cloud mass are being continually blown across the main ridge and they melt quickly as they are borne down over the sunny leeward slopes. I feel assured that on the windward slopes above the lower limit of our area at 4,500 feet there are not any differences of moisture conditions of a kind or amount capable of influencing the vegetation. The cloud blanket gives a uniformity to the conditions, which can scarcely be rendered pronouncedly different by a rise of rainfall from as high an amount as 113 inches to 168 inches per annum.

The percentages of fog during the day at Cinchona are roughly 10 per cent for February, July, and August, and 30 per cent for the other months, and it is to this difference rather than to its slightly lower rainfall of 105 inches that we must look for the basis underlying the principal habitat distinction which I have made—that between the leeward and windward sides of the range. The cloud blanket seldom settles for any length of time over localities on the leeward side below 4,500 feet, and the rapidity with which the rainfall diminishes below that altitude is shown in the 67 inches fall for Resource, which is located south of Cinchona, at 3,700 feet (1,128 meters) elevation.

The fog is of two sorts—a moving, wind-driven, relatively dry fog seldom accompanied by rain, and stationary fog of high humidity and often accompanied by drizzling rain or a heavy downpour. I have observed on several occasions that the moving fog may pass without influence on the humidity of the air. At Cinchona, on the late afternoon of February 28, 1906, I obtained identical psychrometer readings before, during, and after the passage of a wind-blown mass of fog, the humidity being 94 per cent.

The continual high humidity of the Windward Ravines is exhibited in plate 24, figure B, and plate 25, figure B, both of which were secured at the floor of ravines in the vicinity of Morce's Gap. Climatic and topographic conditions join with the sheltering effect of the forest itself and its immense evaporating surface to give to this habitat condition of moistness which can hardly be exceeded in any locality on the globe. The degree to which the surrounding vegetation and its wet surfaces are accountable for the steady maintenance of these high humidity conditions is revealed in the trace shown in plate 24, figure A, which was taken in a tree top 38 feet from the ground and directly above the spot in which the trace in plate 25, figure B, was secured two weeks earlier.

In similar fashion plate 24, figure A, exhibits the play of moisture conditions on a ridge within 500 yards of the location for plate 24, figure B. There was rain all day on Saturday and Sunday, giving the ridge the conditions of a ravine, but on the earlier days of the week fluctuations of humidity were recorded commensurate with those in the tree top. The ridges are exposed to air movements which prevent the attainment of the highest humidities and accelerate the drying of the natural evaporating surfaces of the forest.

The trace shown in plate 26, figure A, exemplifies well the average conditions in Windward Slope forest, being intermediate between ravine and ridge conditions. The greatest fall in humidity, coming just at daybreak, is followed by either a sudden or a gradual rise which is continued through the night.

The humidity conditions of the Leeward Slopes may be judged from plate 23, figure A, and plate 27, figure A. The former was taken in November in the physiological laboratory at Cinchona, a small building with windows and jalousies on all sides; the latter in April, in young ruinate near Cinchona. Both traces exhibit rapid and continuous fluctuations which carry the humidity to relatively low percentages during a large portion of the day. The laboratory and ruinate curves are comparable as respects the localities in which they were taken, but not as respects the months of the year, for the humidity conditions in November may be expected to exceed in every feature those of April (see fig. 1).

Two traces have already been published[1] which go to show that the

[1]Shreve, F. Studies on Jamaican Hymenophyllaceæ. Bot. Gaz. 51 : 184–209. Mar. 1911.

character of the daily humidity curve at Cinchona and in the ruinate is not entirely due to their position on the leeward side of the mountains but must be partly attributed to the fact that both of these localities have been deforested. The traces mentioned were taken at New Haven Gap, on the main ridge of the Blue Mountains, the first in a small clearing, the second in the Windward Slope type of forest which occupies the summit of the gap 200 yards distant. The former resembled the traces taken at Cinchona and in the ruinate; the latter showed a much more constant maintenance of high humidity, and resembled the curves for Windward Slope Forest.

The records secured at Sir John Peak were for the floor of an open stand of *Podocarpus* on the extreme summit (see plate 18). The curve from this location (plate 28, fig. A) is similar to that secured on the Ridge at 5,000 feet (plate 24, fig. A), that is to say, it exhibits a high and rather constant humidity on certain days—those which are rainy or entirely cloudy and on other days shows depressions which are nearly as pronounced and long as those of the Leeward Slopes.

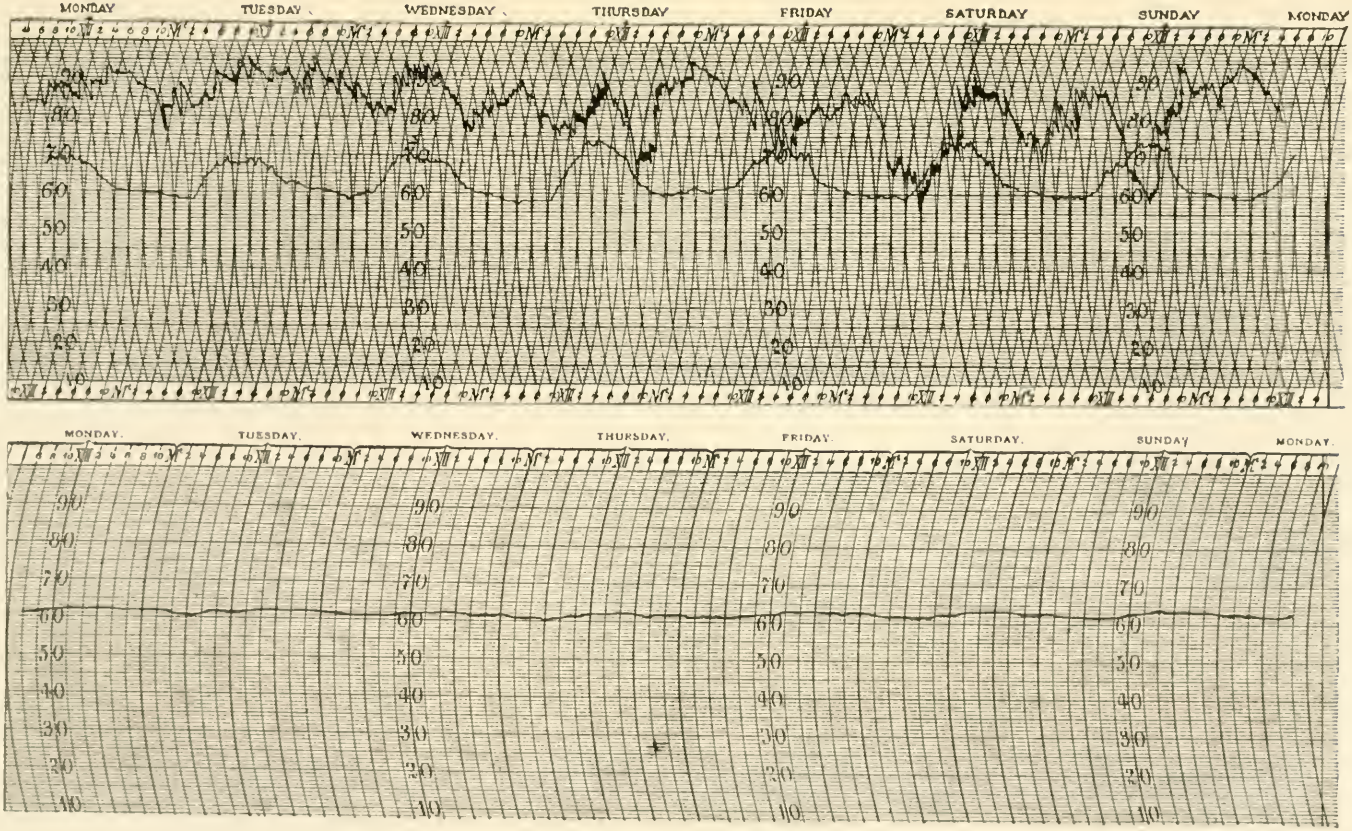
EVAPORATION.

The corrected readings of total weekly evaporation, which were secured in the open air just outside the laboratory at Cinchona and in two stations in the rain-forest, are exhibited in table 10.[1] There is, roughly speaking, an inverse relation between the weekly rainfall and the corresponding amount of evaporation. The highest weekly evaporation rates were 125.1 c.c. for the week ending August 3, and 101 c.c. for the week of November 22, in both of which weeks there was an exceptionally light rainfall. The lowest weekly evaporation occurred in the first two weeks of November, during a period of exceptionally severe precipitation. The average daily evaporation during the weeks of highest and lowest rate were respectively 17.9 and 1.8 c.c.

The Ridge station was located in an open stand of *Cyrilla*, *Tovomita*, *Ilex*, and *Clethra*, and the atmometer was placed on the ground in such a position that it could be struck by the sun's rays during about half of the day, owing to the openness of the forest canopy. The weekly totals of evaporation for this station ranged from a maximum of 41.3 c.c to a minimum of 5.8 c.c., the rate in the former case being slightly

[1]The atmometers used were calibrated by comparison of their rate of loss with that of a standard cup and with the loss from petri dishes. The standard used was Livingston's cup No. 405. The petri dishes were of the standard size, 94 mm. in diameter, and were filled to within 3 mm. of the rim. The readings in terms of No. 405 may be converted into terms of standard No. 200 by multiplying by 0.82. The following figures show the coefficients of correction of the cups used, column A being the original coefficients determined at Tucson, B the coefficients determined at Cinchona in July, C those determined at Cinchona in August, D those at Cinchona in November, and E those found in Tucson after use.

Cup No.	A.	B.	C.	D.	E.	Average of B, C, and D.
294	.....	0.75	0.84	0.73	0.71	0.77
278	0.55	.69	.72	.71	.63	.71
287	.56	.69	.....	.72	.62	.71
307	.64	.....	.....	.71	.71	.71



A. Humidity and temperature record for Physiological Laboratory, Cinchona, for week ending Nov. 12, 1905.
B. Soil temperature record for unshaded grass sod at depth of 1 foot, Cinchona, for week ending Nov. 12, 1905.

higher than that for the corresponding week at Cinchona, and that for the latter week being only one-twelfth that for Cinchona.

The Ravine station was located at the spot shown in plate 1, in the dense shade of tree ferns, above which were growing *Solanum* and *Gilibertia*. The sun was rarely able to strike the atmometer, which was situated on the ground. The evaporation rate in the Ravine was constantly low, fluctuating only between 8.8 c.c. and 2.7 c.c. per week, or 1.2 c.c. and 0.4 c.c. per day respectively.

TABLE 10.—*Rates of evaporation in the Cinchona region, July to November, 1909.*

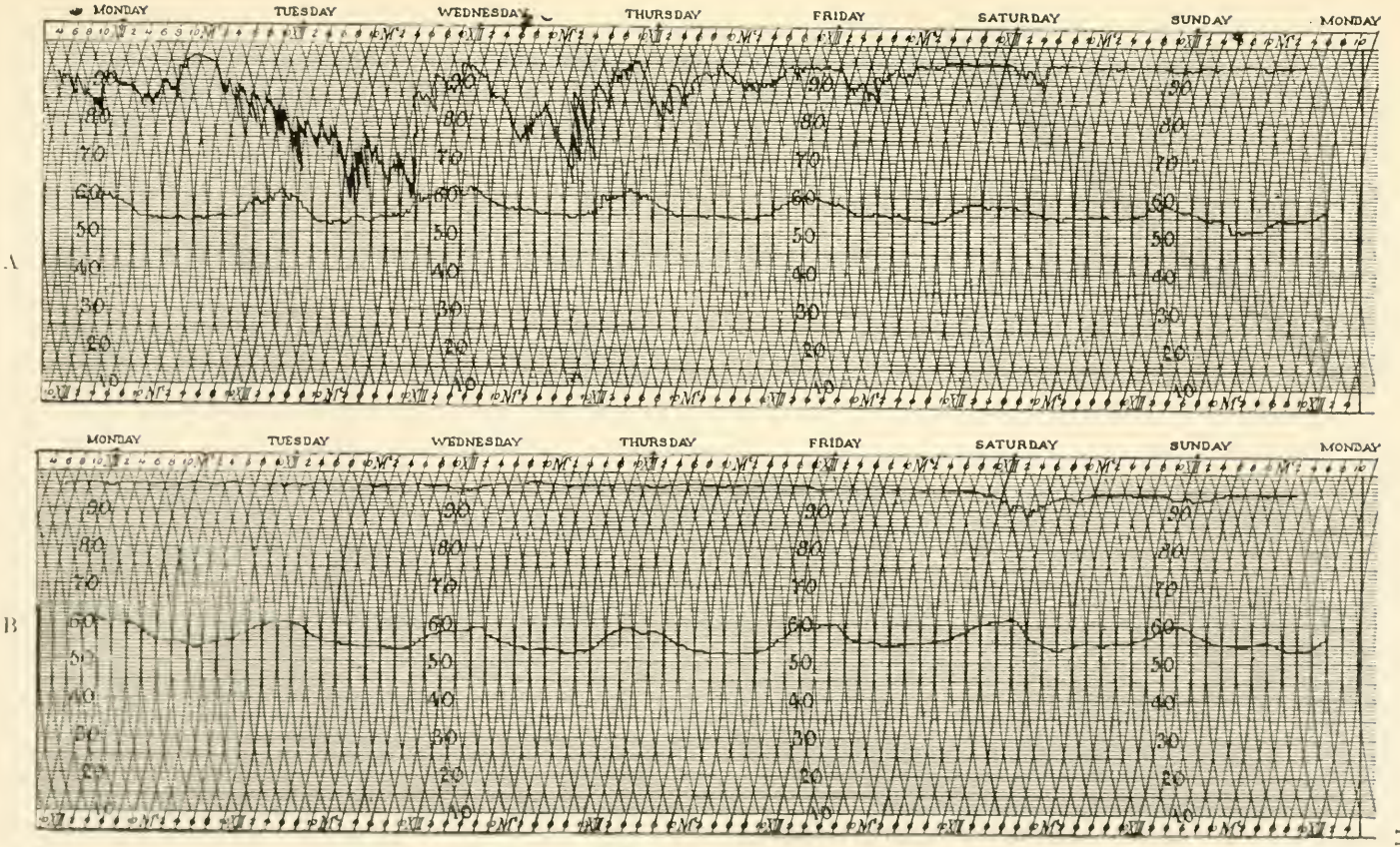
Period ending.	Rainfall, Cinchona.	Evaporation.		
		Cinchona, No. 294, No. 278.	Ravine, No. 307.	Ridge No. 297.
	cm.	*c.c.*	*c.c.*	*c.c.*
July 20.....	6.0	47.6	...	....
27.....	.2	88.0	8.0	....
Aug. 3.....	.3	125.1	8.8	....
10.....	5.0	47.2	3.6	....
17.....	1.8	62.3	6.5	....
24.....	....	....	...	....
31.....	7.4	38.3	4.0	....
Sept. 6.....	15.4	55.5	2.7	16.4
13.....	10.4	62.3	5.7	25.6
20.....	12.7	40.7	4.1	41.3
27.....	19.7	35.4	...	....
Oct. 4.....	6.4	86.0	6.3	37.0
11.....	24.3	74.8	3.0	5.8
18.....	7.3	67.4	....	...
25.....	22.3	25.0	....	...
Nov. 1.....	3.3	61.3	....	...
8.....	114.7	16.7	....	...
15.....	78.2	12.8	....	...
22.....	1.9	101.7	...	....

The addition of the weekly totals of evaporation for all of the weeks in which simultaneous readings were secured at Cinchona and in the Ravine gives 715.6 c.c. and 52.7 c.c. respectively. Reducing the rate of loss in the Ravine to unity gives a value of 13.5 for Cinchona, the average difference between the evaporation in the two localities being slightly greater than the maximum fluctuation of weekly rate at Cinchona (1:9.8). The addition of the weekly totals for the period in which atmometers were running at all three stations simultaneously gives amounts as follows: Cinchona 319.3 c.c., Ridge 126.1 c.c., Ravine 21.8 c.c. Reducing these amounts to terms of the Ravine as unity gives the following relative values: Cinchona 14.5, Ridge 5.7, Ravine 1.0. A value in this series for the Windward Slopes would probably fall between 3.0 and 4.0, which would mean that the total evaporation of the Leeward Slopes at Cinchona is from four to five times as great as that of the Windward Slopes in the vicinity of Morce's Gap.

From the four months' record of evaporation at Cinchona it is possible to make a rough calculation of the total evaporation of the year. The atmospheric humidity is the most important climatic element in determining evaporation rate in the Blue Mountain region, and the average humidity for the four months from August to November is nearly the average for the year (84.9 as against 84.1 per cent). The total annual evaporation may therefore be estimated as not far from three times the amount for the months covered by the accompanying readings. The total of the readings is 989.1 c.c., which may be placed at 1,000 c.c. for the present purpose. The total annual evaporation of 3,000 c.c. must be multiplied by 0.76, the factor by which the loss of the cup is reduced to terms of the loss from a free-water surface in a petri dish. The annual total is thus made about 2,250 c.c., again keeping the calculation in round numbers. The diameter of the petri dish is 94 mm., and the annual loss from its water surface per square centimeter would be 32.6 c.c. The average annual rainfall at Cinchona is 106 inches, or 271 cm. The total annual fall of rain per square centimeter is therefore 271 c.c., which is to 32.6 c.c. as 8.3 is to 1. The rainfall at Cinchona is therefore about eight times as great as the possible evaporation. Since the evaporation at Cinchona was found to be about fourteen times as great as that in typical Windward Ravine, the ratio of evaporation to rainfall for the latter locality is 1:112, if we take no account of the higher rainfall which undoubtedly exists on the windward side of the Blue Mountains An accurately determined ratio of evaporation to rainfall for this extremely hygrophilous habitat would probably be near 1:140.

AIR TEMPERATURE.

Reproductions of some of the thermograph traces secured at Cinchona and in different natural habitats are shown in plates 23 to 28, and a digest of the data given by these curves is presented in table 11. Although no two of the thermograph traces are strictly comparable in the sense of covering the same interval of time, they serve to show the character of the daily march of temperature, and to emphasize the constancy of the temperature conditions not only throughout the day but throughout the several habitats in which they were secured. Only at Cinchona and in the Ruinate on the Leeward Slope was the average maximum temperature above 70° F. On Sir John Peak the average maximum was 60.5° F., which is higher than that of the Windward Ravines over 1,000 feet lower in altitude, and identical with the maximum secured for Ridge forest at the lower altitude. The minimum temperature at Sir John Peak is, however, carried somewhat lower than that of Windward Ravines at lower elevations, in spite of the records on the peak having been secured later in the spring than those in the Ravines.



A. Humidity and temperature record for floor of forest on a Ridge at 5,000 feet altitude, for week ending Feb. 25, 1906.
B. Humidity and temperature record for floor of forest in a Windward Ravine, at 4,750 feet altitude, for week ending March 18, 1906.

The average daily range of temperature is greater at Cinchona and in the Ruinate than it is in any of the forested areas. The Ruinate record was secured in an exceptionally clear and warm week, and its daily mean range probably represents the maximum for the entire region. The daily range at Sir John Peak, 11.3° F., is higher than for any other forested habitat, as might be expected. The Windward Ravines exhibit the lowest ranges of temperature, and those of the Slope, the Ridge, and the forest canopy are greater and of about the same order of magnitude.

TABLE 11.—*Recapitulation of temperature data for different habitats.*

Location.	Elevation.	Week ending—	Plate showing graph.	Air temperature.			Cinchona, 15-year averages for corresponding months.		
				Average maximum.	Average minimum.	Average daily range.	Maximum.	Minimum.	Range.
	feet			° *F.*	° *F.*	° *F.*	° *F.*	° *F.*	° *F.*
Cinchona	5,000	Nov. 12	23–1	72.2	58.3	13.9	68.3	57.3	11.0
Windward ravine	4,950	Feb. 4	25–2	57.3	52.0	5.3	67.0	53.7	13.3
Windward ravine	4,750	Mar. 18	24–2	59.8	52.7	7.1	67.0	53.9	13.1
In top of tree	4,950	Feb. 18	25–1	61.2	52.4	8.8	67.0	53.7	13.3
Windward slope	4,950	Mar. 11	26–1	61.3	51.9	9.4	67.0	53.9	13.1
Ridge	5,000	Feb. 25	24–1	60.5	52.7	7.8	67.0	53.7	13.3
Ruinate	5,000	Apr. 8	27–1	72.0	51.3	20.7	67.5	55.3	12.2
Sir John Peak	6,200	Apr. 30	28–1	60.5	49.2	11.3	67.5	55.3	12.2

Such slight temperature differences are without significance in the differentiation of the habitats within the rain-forest, and are of importance only in so far as they operate conjointly with other factors in affecting transpiration, growth, and other complex activities of plants. The low nocturnal winter temperatures of the highest peaks are sufficiently different from those of the slopes at 4,500 to 5,500 feet to be of significance in the limitation of species, as has already been suggested. In general, however, the role of temperature as a differential climatic factor in the Blue Mountain Region is an extremely unimportant one.

SOIL TEMPERATURE.

Six weekly graphs of soil temperature have been selected from a larger number as exhibiting the most striking differences in this remarkably uniform factor (plates 22 to 28). There is a close correspondence between the mean temperatures of the soil under the open sod of the lawn at Cinchona, in a coffee field with southerly slope and a light covering of weeds, and in the Ruinate (table 12). The substratum in Windward Ravines possesses a soil temperature nearly 10° F. lower than those just mentioned, and the soil on the summit of Sir John Peak, in the Ridge type of forest, is closely like that of the Windward

Ravine. A graph of temperature was secured in the midst of a heavy mass of hepatics and mosses which was serving as the substratum of a number of epiphytic orchids, 10 feet from the ground on a Windward Slope. This epiphytic substratum showed a less daily range of temperature than the air of the same situation during the same week (6.4° F. as against 9.4° F.), and, as compared with the soil in the Windward Ravine, it exhibited the same minimum and a higher maximum temperature. The mean daily range of soil temperature is so slight in all cases as to be without significance. It is less than 2° F. in all habitats excepting the Ruinate, and is only 1.1° F. in the Windward Ravines.

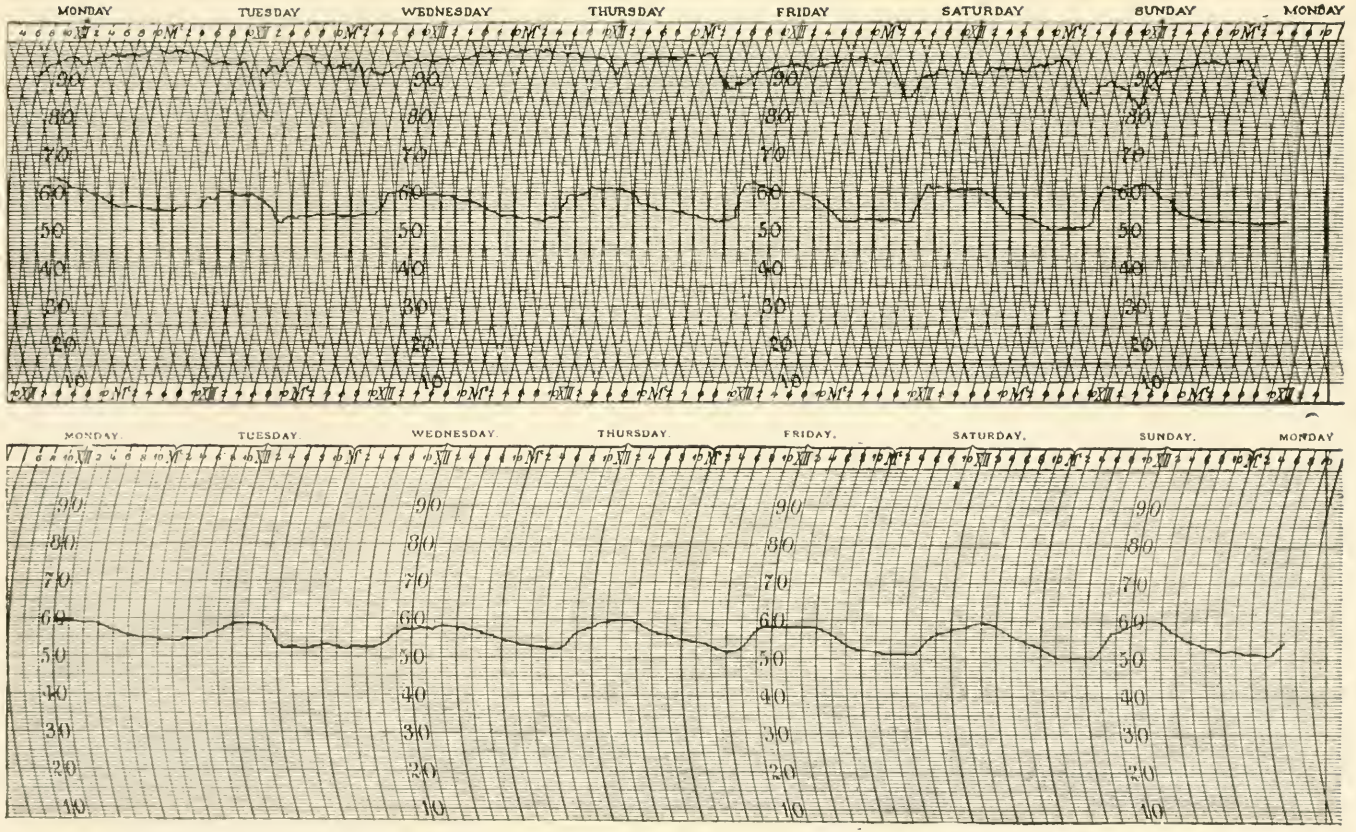
The investigation of the daily march of soil temperature was undertaken partly with a view to investigating the possible relation of the daily march of soil temperature to the activity of hydathodes. The daily

TABLE 12.—*Recapitulation of soil-temperature data for different habitats.*

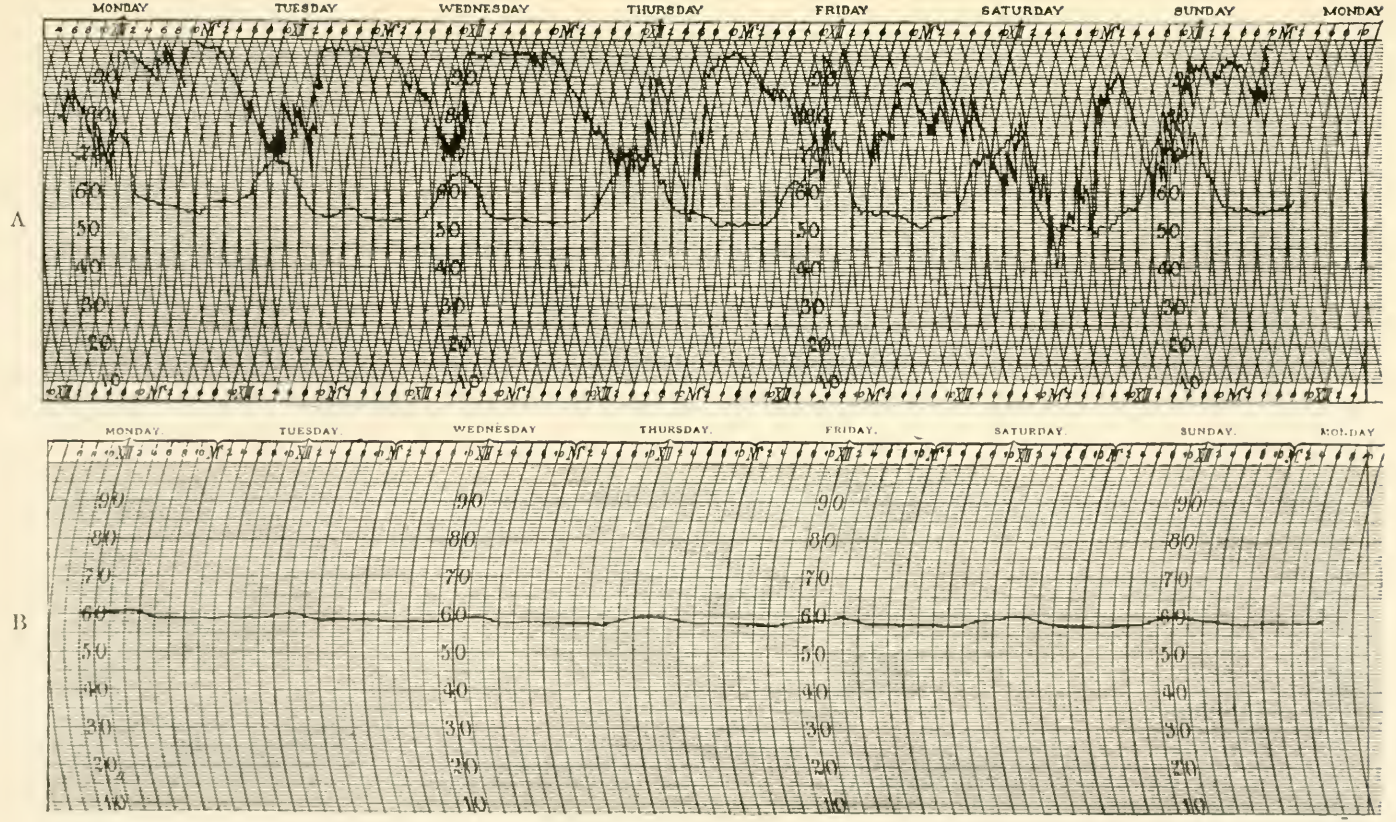
Location.	Elevation.	Week ending—	Plate showing graph.	Soil temperature.			Cinchona, 5-year means for corresponding months.
				Average maximum.	Average minimum.	Average daily range.	
	feet			° *F.*	° *F.*	° *F.*	° *F.*
Cinchona	5,000	Nov. 12	23–2	62.5	60.9	1.6	62.6
Windward ravine	4,900	Mar. 4	29–1	54.0	52.9	1.1	60.5
Epiphytic substratum	4,950	Mar. 11	26–2	59.2	52.8	6.4	60.5
Ruinate	5,000	Apr. 8	27–2	59.7	57.5	2.2	60.4
Coffee field	4,500	Jan. 28	29–2	61.4	59.7	1.7	61.4
Sir John Peak	6,200	Apr. 30	28–2	53.5	52.2	1.3	60.4

range of temperature was found to be so slight and the lag of the daily minimum to be so short that there is no warrant for considering the soil temperature to be of importance in the operation of these structures.

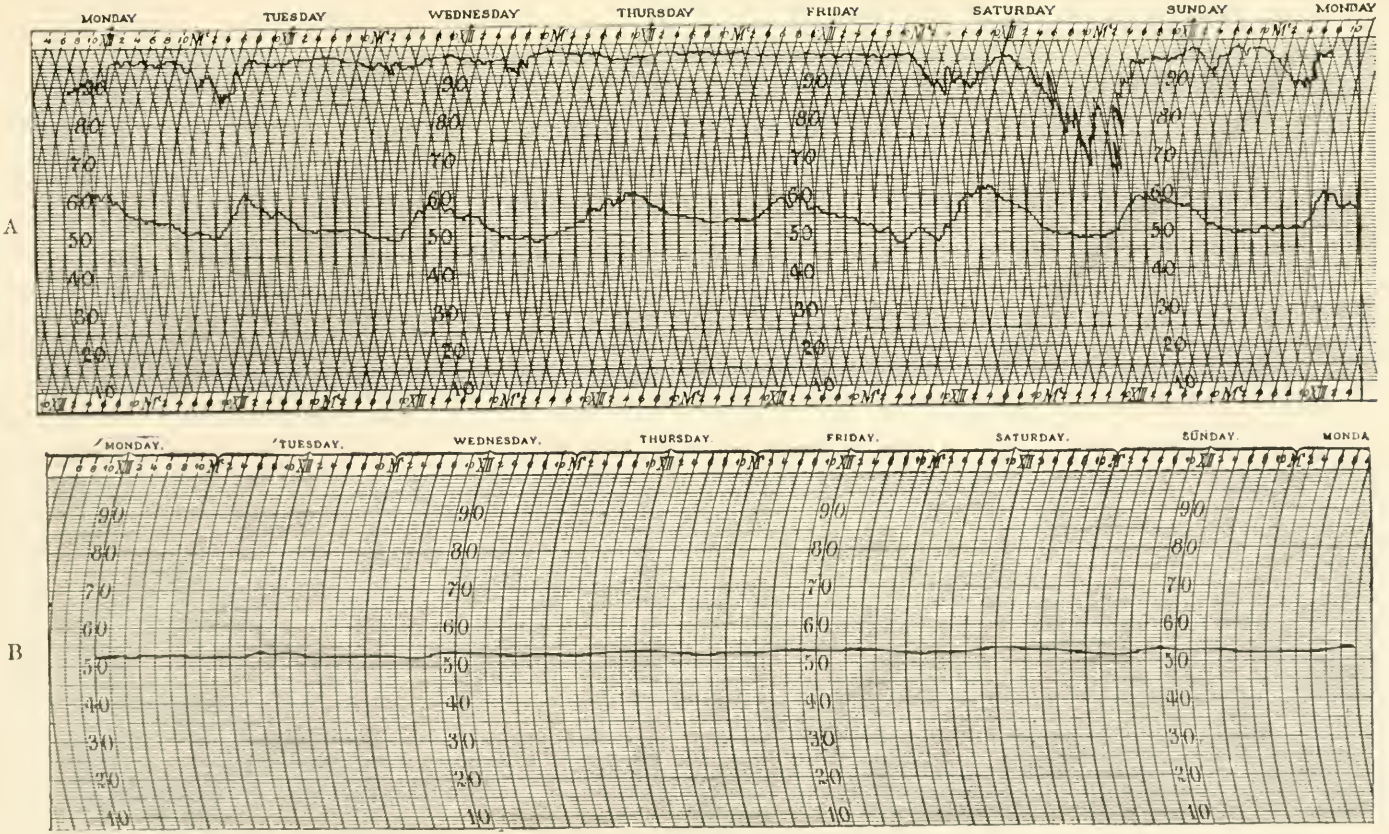
Differences of as much as 10° F., such as exist between the forested soils of the Windward Ravines and the open slopes of the leeward side of the Blue Mountains, are great enough to play a slight role in the distribution of plants, and this difference is perhaps partly responsible for the occurrence of lowland species at higher elevations on the leeward than on the windward side. Aside from this greatest difference in soil temperature, the factor is of no importance in the differentiation of habitats nor in the explanation of plant activities, and its measurement is of relatively little value in this region.



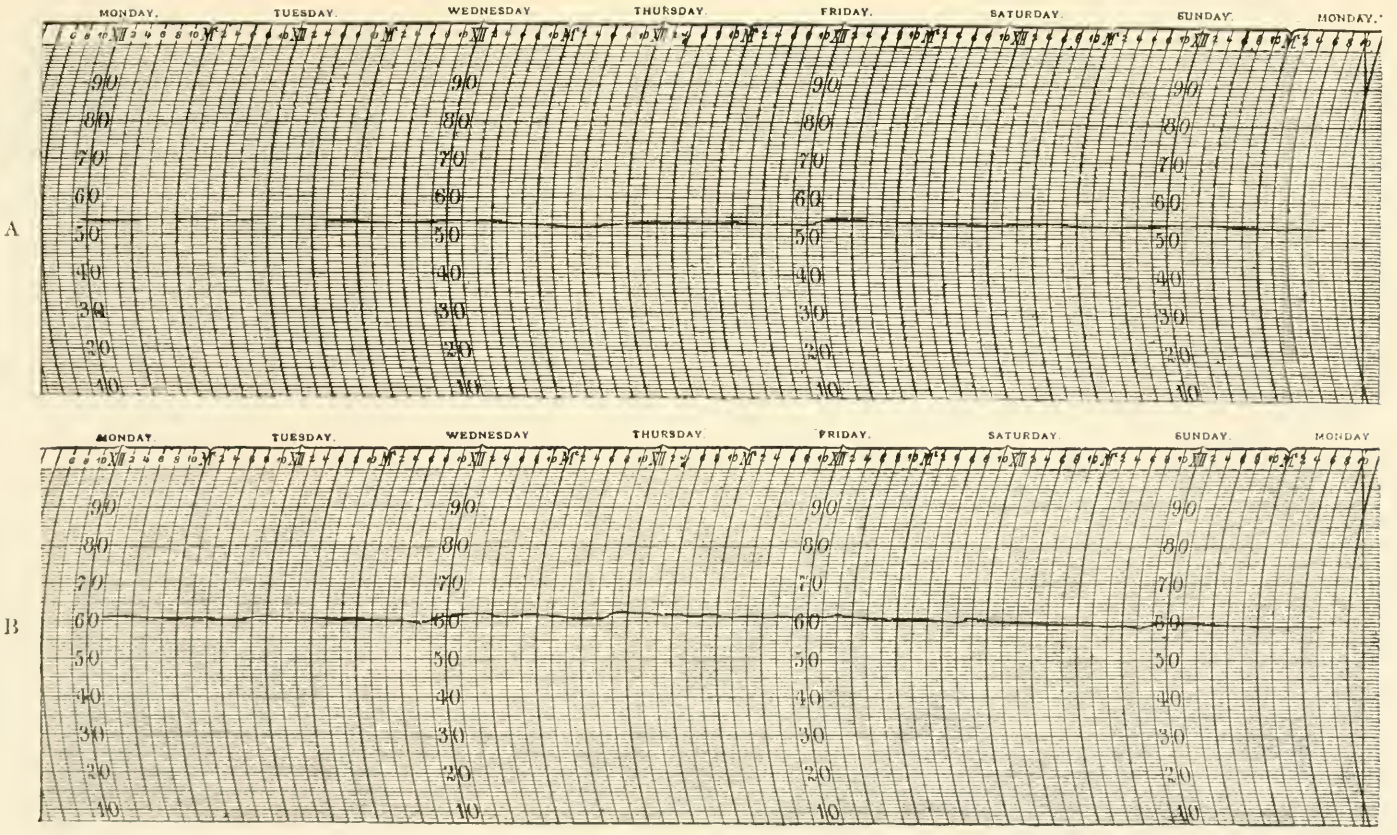
A. Humidity and temperature record for Windward Slope Forest with western exposure, at 4,950 feet altitude, for week ending March 11, 1906.
B. Temperature record for a bed of hepatics which formed substratum of a dense colony of epiphytes 10 feet from ground at same spot in which the record in A was obtained, for week ending March 11, 1906.



A. Humidity and temperature record for young ruinate near Cinchona on a Leeward Slope, for week ending April 8, 1906.
B. Soil-temperature record for same place and time as A.



A. Humidity and temperature record for forest on summit of Sir John Peak, about 6,200 feet, for week ending April 30, 1906.
B. Soil-temperature record accompanying the above.



A. Soil-temperature record for bed of a Windward Ravine at 4,900 feet altitude, for week ending March 4, 1906.
B. Soil-temperature record for a coffee field on leeward slope at 4,500 feet, with southern exposure, for week ending January 28, 1906.

SEASONAL BEHAVIOR OF RAIN-FOREST VEGETATION.

The relative constancy of temperature in the Blue Mountain Region, together with the lack of a pronouncedly dry season, gives the perennial plants of the rain-forest continuously favorable conditions for vegetative and reproductive activity in so far as concerns these major factors of the climatic environment. During my two sojourns at Cinchona I became interested in the seasonal variations of activity in the native trees and shrubs, and made observations which collectively cover all months of the year excepting June. The resulting data exhibit a diversity of behavior which would not be expected on *a priori* grounds in a region of such climatic constancy. There is, however, a season of relative rest in both vegetative and reproductive activity from October until January. In these months there occurs a total or partial fall of leaves from a few species of trees, and a small total mass of growth and bloom in the woody vegetation as a whole. It is significant that the months named are the most rainy and the most heavily clouded months of the year, a consideration of far more importance than their slightly lower temperature. From February to September there is greater activity, and it is in these months that the divergent behavior of the various forms is manifested. There are several species in which the winter is not a season of growth rest, but greatly outnumbering them are the plants in which the spring and early summer are the time of greatest shoot and leaf formation. The increasing number of sunny days in the months which follow the close of the winter rainy season is equivalent to a much greater rise of temperature for the plants than is indicated by the thermometrical shade readings, and may well be responsible for an increased vegetative activity which wanes considerably before the advent of midsummer.

Following are described the principal features of the seasonal behavior of the Blue Mountain vegetation.

I found growth and blooming to go on continuously at all months of the year in a number of under-trees and shrubs, including the following:

Piper geniculatum.
Piper fadyenii.
Bœhmeria caudata.
Boeconia frutescens.
Dodonæa angustifolia.
Malvaviscus arboreus.
Heterotrichum patens.
Oreopanax capitatum.
Acnistus arborescens.
Datura suaveolens.

In *Oreopanax capitatum* there is a short check in activity in midwinter. In *Datura suaveolens* blooming occurs at intervals of three to six weeks throughout the year, being sometimes followed by a complete fall of leaves.

A few of the larger trees also continue their activity throughout the year:

Ilex montana var. occidentalis.
Solanum punctulatum.
Psychotaria corymbosa.
Miconia quadrangularis.

In certain forms growth and leaf formation are continuous, while blooming occurs at a definite season, as in

Alchornea latifolia.
Cestrum hirtum.
Brunellia comocladifolia.
Sciadophyllum brownei.
Gilibertia arborea.

In all these forms a check in growth may be noticed in flowering shoots. In a few trees which otherwise grow continuously there may be noticed a check to growth for some months during the maturing of fruit, owing to the inflorescence being terminal, as in *Cithatexylum caudatum* and *Miconia rubens*, both of which bloom in the autumn and mature fruit during the winter, thereby sharing in the growth rest of some trees which are not in fruit at the time.

The winter rest is most marked in those trees which lose their leaves and remain bare for several weeks, which are:

Rhamnus sphærospermus.
Clethra alexandri.
Clethra occidentalis.
Viburnum villosum.
Viburnum alpinum.

Some trees of *Clethra occidentalis* retain a few of their leaves, while trees of *Clethra alexandri* are often bare for a week or two. Among the above, and the trees which cease growth but do not lose their leaves entirely, there are well-marked terminal resting buds, covered by scale leaves of thin texture.

The trees which bloom between the last week of January and the end of May are the following:

Podocarpus urbanii.
Hedyosmum arborescens, January.
Myrica microcarpa, March to April.
Alchornea latifolia, March to April.
Acalypha virgata, February to May.
Ilex obcordata.
Turpinia occidentalis, May.
Rhamnus sphaerospermus, March to April.
Haemocharis haematoxylon, Feb. to April.
Cleyera theoides, January.
Clusia havetioides.
Eugenia fragrans, February.
Eugenia marchiana, February.
Meriania purpurea, March and April.
Miconia quadrangularis.
Mecranium purpurascens.
Gilibertia arborea, May.
Gilibertia nutans, May.
Garrya fadyenii.
Vaccinium meridionale, Jan. to March.
Cestrum hirtum.
Cestrum sp.
Viburnum villosum, Feb. to March.
Viburnum alpinum, Feb. to March.

In some of the above the flowers are borne on the wood of the season, more particularly in those which bloom late, after growth has had time to progress, as in *Turpinia occidentalis*, *Gilibertia arborea*, and *Gilibertia nutans*. Much more commonly the flowers are borne on the wood of the preceding season. In the majority of cases shoot and leaf growth are simultaneous with the growth and unfolding of the inflorescence, that is, both cease before the coming of summer.

In trees of constant growth the leaf-fall is likewise constant, and it is difficult to determine the age of leaves at fall unless they are very short-lived. In *Bœhmeria caudata* a calculation based upon the interval of time between the first appearance of successive pairs of leaves on a shoot and the number of pairs persisting on shoots showed the leaves

to be from five to seven months old at fall. In other constantly growing forms the leaves apparently range from seven to twelve months in duration.

In the trees which have a marked vernal growth leaf-fall is continuous throughout the year in one, *Cyrilla racemiflora*, and is gradual throughout the summer in *Myrica microcarpa*, *Turpinia occidentalis*, and *Gilibertia arborea*. In *Vaccinium meridonale* the leaf-fall follows immediately upon the reaching of mature size by the leaves of the next succeeding spring, and proceeds rapidly so as to be complete by the end of April. Yet on the flowering shoots, where new shoots and leaves are not formed, the old leaves persist, so that we have leaves of the year and leaves of the preceding year functioning side by side. In *Podocarpus urbanii* the leaves of the previous year frequently persist on certain shoots, although they rarely remain until the third year. With the exception, then of *Vaccinium* and *Podocarpus*—not to mention the scale-leaved *Juniperus barbadensis* and *Baccharis scoparia*—there are no trees in the Blue Mountains on which the leaves persist for much more than twelve months. Among the shrubs the species of *Wallenia* are the only forms with leaves of more than one year's persistence, but I am unable to state their length of life.

The species which bloom during July and August are the following:

Weinmannia pinnata.
Brunellia comocladifolia.
Guarea swartzii.
Mettenia globosa.
Cyrilla racemiflora.
Eugenia biflora var. wallenii.
Sciadophyllum brownei.
Lyonia jamaicensis.
Turpinia occidentalis.

The forms flowering from October to December are:

Nectandra patens.
Miconia rubens.
Clethra occidentalis.
Rapanea ferruginea.
Palicourea crocea.
Citharexylum caudatum.
Baccharis scoparia.

In connection with the behavior of the native winter-deciduous species I have been interested to observe the periodic activities of several north temperate trees planted in the grounds at Cinchona. In the European *Quercus robur* definite resting buds are formed in the late summer but the leaves are not shed during the autumn—are indeed persistent in part until the following May. The resting buds swell during December and January and new shoots may be observed here and there over the tree during the entire spring, flowers being also borne during this long period of irregular activity. *Liquidambar styraciflua* also retains its foliage throughout the winter, new shoots forming as early as February and continuing for two months, while there is a gradual fall of the old leaves. In *Liriodendron tulipifera* growth and leafing are continuous through the summer and into October, but during the autumnal rains the leaves, old and new, are shed, leaving the tree bare until the middle of February. Flowering takes place during April and May. *Taxodium distichum* retains its

winter-deciduous habit, losing its leaves in October, not to renew them until late February or early March.

Here, then, is a group of four north temperate deciduous trees which have almost identical foliation and defoliation behavior when found in their natural ranges, but exhibit considerable diversity when brought into the climate of Cinchona.

There is no locality on the globe which possesses a completely uniform climate throughout the year, and consequently no locality in which vegetation fails to be subject to the influences of fluctuating physical conditions. When the climate of the Blue Mountains is contrasted with the climate of such a region as the eastern United States it is made to seem uniform, in spite of its small annual fluctuations. The vegetation of the eastern United States is correspondingly marshaled into a unison of seasonal behavior, while the plants of the Jamaican mountains show only a slight tendency to such a marshaling (as indicated by the predominance of spring flowering and growth) in accord with the slight changes of physical conditions from season to season. In short, the more striking the differentiation of the two or more seasons of the year in a given locality, the more striking is the unison of vegetative and reproductive behavior in the vegetation; the less pronounced the diversity of the seasons, the nearer does the vegetation approach the appearance of unbroken activity, an appearance regarding which we still know little, and shall continue to know little until the entire subject of periodic phenomena is attacked by experimental methods.

RATE OF GROWTH IN RAIN-FOREST PLANTS.

Our knowledge of the rate of growth of tropical plants is nearly confined to the results of measurements which have been made on leaves and stems of lowland plants in which the rates are conspicuously high. Lock[1] found a rate of elongation of 231 mm. per day in the shoots of the giant bamboo, *Dendrocalamus*, in Ceylon, and Maxwell[2] observed a rate of 107 mm. per day in the growth of banana leaves. Schimper[3] measured the leaves of *Amherstia* and some other tropical lowland trees and found their rates of growth to be exceedingly rapid. Such high rates of growth have been tacitly credited to all tropical plants, although there are doubtless very many lowland forms in which the usual rates of growth are relatively slow, while slower rates are naturally to be expected in montane tropical regions.

Only a few weeks of observation in the Cinchona region were necessary to convince me that the rates of growth in the native rain-forest vegetation are relatively slow, and that the physical conditions under which they exist are not such as would be conducive to rapid rates. I became interested therefore in the growth behavior of the vegetation, as a summation of the many and less easily measured fundamental activities of the plants, and made both observations and measurements with a view to increasing our knowledge of plant activity in a region which presents equable conditions of temperature and almost uniformly favorable conditions of moisture.

Attention has already been called to some of the seasonal differences in growth activity which exist between the various species of the rain-forest. It is natural to anticipate differences of rate between plants in which growth is continuous and those in which it is taking place during only a few months or weeks of the year; and there are a few cases in which such differences exist. The growth of *Gilibertia* and *Turpinia* is confined to a few weeks in the late spring, and is one of the most rapid growth phenomena in the rain forest. In *Cyathea pubescens* and other tree ferns the formation of new leaves takes place during the winter and spring, and their elongation is the most rapid growth phenomenon that has come under my notice. The elongation of leaves in all terrestrial ferns is much more rapid than the rate of growth in the leaves of other herbaceous plants, and this is due to the seasonal character of the growth of fern leaves and to the reserves in the rhizones through which the rapid growth becomes possible.

Marked branches of individual trees of several common species were kept under observation from February until May 1906, and with the exception of *Gilibertia* and *Turpinia* none exhibited rapid growth.

[1]Lock, R. H. On the Growth of Giant Bamboos. Ann. Roy. Bot. Gard. Peradeniya, 2, pt. 2, August 1904.

[2]Maxwell, W. The Rate of Growth of Banana Leaves. Bot. Centrb., 67, 1896.

[3]Schimper, A. F. W. Plant Geography, Oxford Edition, 1903, p. 218.

On the shoots of *Hedyosmum arborescens* and of *Podocarpus urbanii* which were under observation no new leaves were formed, although the shoots were favorably situated as respects light and their position on the tree. In *Clethra* and *Viburnum* the leaves which appeared after the mid-winter defoliation of the trees grew less rapidly than the leaves of *Alchornea*, which is in continual activity, and made in a week about the same increase in size that may be made in a single day by the leaves of a maple in the eastern United States in April or May.

Owing to the slowness of shoot growth I have confined my measurements to leaves. During the spring of 1906, from February to May, I made determinations of growth rate in *Bœhmeria caudata, Alchornea latifolia, Clethra occidentalis, Tovomita (Clusia) havetoides, Pilea nigrescens*, and *Cyathea pubescens*.[1] Additional measurements were made in 1909, from July to October. The measurements at both times were commonly made at fortnightly intervals.

TABLE 13.—*Maximum rates of leaf growth in rain-forest plants.*

When measured.	Rates, mm. per day.						Average.
1906, February to May:							
Bœhmeria caudata	3.86	4.40	....	....	....	...	4.13
Alchornea latifolia	2.46	2.50	1.81	2.91	2.26	...	2.38
Clethra occidentalis	2.06	2.06	1.74	1.56	....	...	1.82
Tovomita havetioides	1.26	.95	....	....	....	...	1.10
Pilea nigrescens	.33	.46	.38	....	....	...	.39
Cyathea pubescens	32.7	48.9	49.4	37.2	....	...	42.00
1909, July to October (to September for Pilea):							
Pilea nigrescens No. 1	.43	.41	.43	....	....	...	.42
Pilea nigrescens No. 2	.20	.29	....	....	....	...	
Pilea nigrescens No. 4	.43	.60	.57	.29	.34	.61	
Peperomia basellæfolia	1.14	1.35	1.06	1.00	.93	...	1.10
Asplenium alatum (fronds)	3.57	4.71	4.86	....	....	...	4.38
Asplenium alatum (pinnæ)	.57	.50	.29	....	....	...	.45

The growth of each leaf is at first slow, reaches a maximum at about one-fourth to one-half its mature size, and then falls to a much slower rate. The most rapid maximum rates that were discovered in the measurements of 1906 were 4.4 mm. per day for *Bœhmeria*, 2.9 mm. for *Alchornea*, and 49.4 mm. for the unfolding leaves of *Cyathea*. The slowest maximum was for *Pilea*—0.33 mm. per day. The measurements of 1909 were made only on *Pilea, Peperomia basellæfolia*, and *Asplenium alatum*. The maximum rates for all leaves measured in 1906 and 1909 are given in table 13.

The fact that *Pilea nigrescens* is the commonest herbaceous plant on the floor of the rain-forest, ferns excepted, and the fact that it exhibited the slowest rate of growth of any of the plants brought under measurement, led me to make a more extended series of observa-

[1]Shreve, F. Rate of Growth in the Mountain Forests of Jamaica. Johns Hopkins Univ. Circ. No. 195, March 1907.

tions on it than on any of the other species. Plants of *Pilea* seldom exceed a height of 50 cm. (20 inches), and maintain a smooth green epidermis on their oldest stems. The leaves are opposite and commonly reach a mature size of 40 to 60 mm. in length, and are approximately half as broad as they are long. Two or three pairs of juvenile leaves may frequently be found on the lowest nodes of plants which have reached the usual size, such leaves being nearly orbicular and from 8 to 15 mm. in diameter. The inflorescences of *Pilea* are axillary, and their existence and growth are found to have no retarding effect on the growth rate of the leaves by which they are subtended.

All plants of *Pilea* on which growth measurements were made in 1906 and in 1909 were situated on the floor of a Windward Ravine, and were selected with a view to securing plants of average size and full vigor. The maximum rates of elongation are given in table 13. The entire series of rates of growth has been grouped according to the length of the leaf at the beginning of each interval of measurement—the first group comprising the rates in leaves less than 10 mm. in length, the second those from 10 to 20 mm. in length, and so on by 10 mm. intervals to 60 mm. The averages of the groups of rates give data for a curve of growth rate, from which it is possible to learn the mean rate of leaf growth at six successive stages in elongation. The averages are expressed in millimeters per day in table 14.

TABLE 14.

Length of leaf.	Average growth.
mm.	*mm.*
0 to 10.....	0.36
10 20.....	.38
20 30.....	.30
30 40.....	.28
40 50.....	.19
50 60.....	.18

From these rates of growth it is possible to determine the average length of time required for a leaf to reach its mature size. Leaves which attain a length of 40 mm. are 118 days old at maturity; those growing to 50 mm. in length may be as old as 168 days, while those reaching the maximum size at 60 mm. are probably 218 days old at full maturity of size. It is possible that some of the leaves of maximum size make a growth above the average rate throughout their development, and thus reach the mature size in more than 118 days and less than 168. It has been commonly found, however, that large leaves continue to grow at a very slow rate, and it is on the basis of the growth rate of such leaves that the computation of 218 days is made.

The growth of a new pair of leaves begins at about the time that the next pair below them are half grown. The plants on which measurements were made had from seven to twelve pairs of leaves. If the leaves of these plants are assumed to have reached half their mature size in sixty days, as would be the case if all leaves made the most rapid growth, the age of the plants may be roughly estimated at from fourteen to twenty-four months. Below the sixth or seventh node from the tip it is a common thing to find that some of the leaves have

fallen. Those on the sixth node will have been about one year old at fall, and those which still adhere to the lower nodes may be of any age up to two years. The lowest of the larger leaves are quite commonly covered with epiphyllous hepatics.

A more exact measure of the growth of *Pilea* in terms of the size of the plant was secured by making a computation of the relation which was borne by the new to the old extent of leaf surface in two plants that were under fortnightly observation and measurement, from the middle of July to the middle of September. On the completion of the measurements of these plants their green weight was secured and their leaf area was determined by the method commonly used in transpiration experiments. In the first plant eight leaves were in course of growth from July to September, in the second plant twelve leaves. The area of all the leaves on each plant in July was determined by using the September area of all the mature leaves and an approximate area for the leaves which had grown. This approximation was made by considering each leaf as an ellipse, with the length and width in July as the axes. The actual areas in September, the calculated areas in July, and the amounts of growth are shown in table 15. The extent of new leaf surface was 9.0 per cent that of the old in the first plant and 12.3 per cent in the second. In the lack of similar data for any other rain-forest species or for the plants of any other region I am unable to make any comparison of these figures with the performance of other plants.

TABLE 15.—*Rate of leaf growth in Pilea nigrescens.*

	Fresh weight of top.	Total area, September.	Growth in area.	Area, July.	Growth, as percentage of July area.
	grams	*sq. cm.*	*sq. cm.*	*sq. cm.*	*p. ct.*
Pilea No. 1.....	11.74	236.7	19.6	217.1	9.0
Pilea No. 2.....	10.07	263.3	28.9	234.4	12.3

In size and habit *Pilea nigrescens* closely resembles *Pilea pumila* of the eastern United States. The plants of the former species which are from one and a half to two years old are scarcely larger than the plants of *Pilea pumila* which have grown from seed, germinating in late April or early May, and have reached mature size in July or August. In other words, the American species makes from six to eight times as rapid development as the Jamaican species.

There is no mathematically exact reciprocal relation between the growth rate and average transpiration rate of the plants in which both of these phenomena have been studied; indeed, it would be worth while to seek such a relation only after the use of more exact methods of growth measurement and more careful measurement of physical conditions. There is every reason to believe, however, that the low rates

of growth exhibited by rain-forest plants are occasioned by low rates of transpiration and adverse conditions for photosynthesis, the former being due chiefly to the prevailing high humidities and the latter to the high percentages of cloud and fog. The fact that growth is slower in the montane than in the lowland regions of the tropics is not surprising, since, in addition to the factors mentioned, temperature differences also enter the complex in favor of more rapid growth in the lowlands.

TRANSPIRATION BEHAVIOR OF RAIN-FOREST PLANTS.

METHODS AND MATERIAL.

The work reported in the succeeding pages was directed to an investigation of the amounts and behavior of transpiration in characteristic montane rain-forest plants. The object kept in mind in planning the experiments was to secure results that would at once contribute to a precise knowledge of transpiration in the plants of an extremely moist region, and at the same time elucidate some of the local features of plant distribution as related to the physical characteristics of the habitats which had already been under investigation.

Through the use of atmometric observations I have been able to institute a strict comparison between series of transpiration readings taken at different times and between the conditions of the field and the laboratory. The securing of simultaneous readings of transpiration and evaporation makes possible also the comparison of transpiration amounts and behaviors in plants of widely separated localities, with a basis of accuracy which removes this subject from the limbo of controversy into which botanical literature has sometimes seen it descend.

The work on transpiration comprised the determining of (*a*) the daily march of the rate of water loss under the natural conditions of a montane tropical region, (*b*) the effect of high humidities and of darkness on the rate, (*c*) the comparative amounts of stomatal and cuticular transpiration in the slightly cuticularized and thin-walled leaves of rain-forest plants, (*d*) the behavior of stomata as affecting the rate of transpiration, (*e*) the comparative transpiration rate and transpiration behavior of different types of rain-forest plants as simultaneously measured, and (*f*) the daily march of the relative transpiration[1] rate.

The plants used in these experiments were *Alchornea latifolia* and *Clethra occidentalis*, two of the commonest trees in the rain-forest; *Dodonæa angustifolia*, one of the commonest shrubs on the Leeward Slopes of the Blue Mountains; *Peperomia basellæfolia*, a thick-leaved herbaceous plant of the open Ridge forests; *Pilea nigrescens* and *Peperomia turfosa*, characteristic herbaceous plants of the floor of the Windward Slopes, and *Diplazium celtidifolium* and *Asplenium alatum*,

[1]The term "relative transpiration" is used in the sense in which it was employed by Livingston (Carnegie Inst. Wash. Pub. 50) to denote the ratio of transpiration to evaporation.

extremely hygrophilous ferns of the narrowest Windward Ravines. The five herbaceous species last named were chosen as being the most characteristic plants of the three habitats of the rain-forest which differ most pronouncedly in general moisture conditions, as well as being suited to the requirements of experimentation.

In work with *Alchornea*, *Clethra*, and *Dodonæa* only cut shoots were used, and the potometer method was required for measurement of their transpiration. The greater part of the work was done with potted plants of the herbaceous species, and by the method of weighing sealed pots. The material used in 1909 was potted two months in advance of my arrival at Cinchona, and kept in the shade of a row of bamboos, I was thereby supplied with a set of vigourous plants in normal condition.

Nearly all of my experimentation was carried on in the physiological laboratory building of the Tropical Station at Cinchona, which is admirably suited for such a purpose. This building is about 12 by 24 feet in size, provided with a deep wall table, above which the sides of the building are completely occupied with alternating glass windows and open windows provided with jalousies. The light conditions are practically like those of the floor of the forest, and the temperature and humidity follow the outdoor shade conditions of the Leeward Slope both quickly and closely. Plants subjected to continuous darkness were placed in a small closet under the wall table, which was made light-tight by using a double jacket of plant driers. The arrangement of the jackets was such as to provide ventilation, and the size of the closet was great enough to enable me to get inside it and thereby to assure myself of its darkness. A moist closet was used, which was made of window sash and placed next to one of the windows of the laboratory. Portions of its sides were covered with plant driers, kept constantly wet, and its floor was covered with sphagnum moss. It was possible to keep the humidity of this closet between 90 and 95 per cent without difficulty.

The woody shoots used in transpiration experiments were in each case cut under water and allowed to stand in water from six to ten hours before use. The potted plants were prepared for use by covering the pots with plastocene, over which was rubbed a thin coating of vaseline. The pots were not sealed at the bottom, but were placed in saucers for convenience in handling. A water-tight joint was then made around the circumference of the base (see plate 21 B). This made it possible to use a potted plant a second time by removing it from the saucer, taking off the cardboard top (covered with plastocene), and giving it a "rest" of several days.

The moisture of the soil in which my potted plants were growing was not precisely determined in connection with the transpiration series in which they were run. The soil used had been made up in such a way as to be uniform for all the pots, and each group of pots

brought into the laboratory for experimental use had been subjected to the same frequent rainfall. The soil in which the plants were rooted was, therefore, like that of the open, extremely moist, and the lowering of moisture content to which it was subjected by the plants during the course of any one experiment was too slight to be thought of as affecting the transpiration rate. Most series were run for two days without opening the sealed pots, but in several other cases the same plants were opened at the top and bottom, set outdoors for a few days, and then used again.

For the short intervals of the transpiration experiments evaporation was measured by weighing a porous cup atmometer, mounted in a small glass jar (see plate 21 B). This method was more satisfactory than the use of a burette, not only because of its greater accuracy, but because it obviated the error due to the expansion and contraction of the water column of the burette at morning and night.

The area of leaf surface was determined by making blue prints of the fresh leaves, cutting and weighing in the usual manner. The figures given for area of leaf surface are twice the area of the blue prints, except in the case of leaves coated at top or bottom. The total transpiration of a leaf is therefore divided equally, in calculation, between the upper and lower surfaces.

All readings of transpiration in the following tables are given in terms of the loss in milligrams per hour from a square centimeter of leaf surface, and the evaporation amounts are reduced from the atmometric readings to losses per hour in milligrams from a square centimeter of free water surface. In plotting the diagrams the evaporation has been divided through by 4 or by 10, as is indicated on each curve, it being thereby possible to condense the diagrams. The readings given opposite each hour are for the period closing at that hour, and the length of the period is indicated by the hour given on the preceding line of the table. The first hour given in each table is that at which the series was set. In the diagrams the readings are plotted to the ends of the hours.

The stomatal readings given in connection with several of the transpiration series were made by the method used by Lloyd in his work on *Fouquieria*.[1] The method was used in the manner recommended by Lloyd, and the precautions mentioned by him were all taken, in order to give this means of direct stomatal observation a thorough test. Merck's absolute alcohol was used, and the supply bottle was kept free of moisture by introducing a considerable quantity of dehydrated copper sulphate. Livingston and Estabrook[2] found that it is unnecessary to use absolute alcohol in the operation of this method, and that essentially identical results are secured with grades of alcohol

[1]Lloyd, F. E. The Physiology of Stomata. Carnegie Inst. Wash. Pub. 82, 1908.

[2]Livingston, B. E., and Estabrook, A. H. Observations on the degree of stomatal movement in certain plants. Bull. Torr. Bot. Club 39 : 15–22, 1912.

as low as 90 per cent. Lloyd attributes the efficacy of absolute alcohol in the fixation of stomata to its rapid dehydrating power, and found that the presence of a layer of mesophyll cells beneath a piece of epidermis which had been treated to absolute alcohol affected the openness of the stomata. I have found the openness to be little affected by underlying pieces of mesophyll thin enough to permit measurement of the stomata above them. It would appear, then, either that grades of alcohol below absolute are sufficiently active in dehydration to fix the walls of the guard cells, or else that the principle involved in this method is not that from which Lloyd started in the development of it.

My measurements of stomata have been made in microns and the averaged values for each reading are given in the tables. I have commonly read 24 stomata in each preparation, and have found that two such series agree within 1 to 6 per cent, in spite of the variability of the openness to which I shall draw attention. The stomatal datum used in plotting is the square root of the product of length and width of the averaged readings. This gives a figure which is proportional to the diameter of a circle of the same area, and is used in conformity with Brown and Escombe's law of the static diffusion of gases.[1]

DAILY MARCH OF TRANSPIRATION.

The daily march of transpiration has been ascertained for eight species: *Alchornea latifolia*, *Clethra occidentalis*, *Dodonæa angustifolia*, *Pilea nigrescens*, *Peperomia turfosa*, *Peperomia basellæfolia*, *Asplenium alatum*, and *Diplazium celtidifolium*. This group of species is representative of the trees, shrubs, herbaceous flowering plants, and hygrophilous ferns of the rain-forest. The several days on which the determinations of transpiration march were made were somewhat unlike as respects weather conditions, but varied only slightly around the normal type of day that has already been described as characteristic of the region (p. 17). The principal feature of the daily weather conditions that impresses itself on the curve of transpiration is the hour at which the clearness of the early morning is terminated by clouds or floating fog from the main ridge of the Blue Mountains. The daily curve of evaporation is influenced by the same variable weather conditions, and its shape for a given day bears a rather constant relation to the daily curve of transpiration.

The maximum transpiration for the day may occur as early as the period from 8 to 9 a. m., as is shown for *Clethra* and *Alchornea* in Experiment 1 (table 16, fig. 2), and for *Dodonæa* in Experiment 2 (table 17, fig. 3). More commonly the maximum occurs between 10 and 12 a. m., or is sometimes registered as late as 1 p. m. in two-hour readings taken so as to terminate at that hour (see tables 17, 18, 19 and 20). On the days which remain permanently or intermittently cloudy after the first obscuring of the sun, the transpiration shows a

[1]Brown, H. J. and Escombe, I. Static Diffusion of Liquids and Gases in Relation to the Assimilation of Carbon. Phil. Trans. Roy. Soc. London, 193 : 283–291, 1900.

single pronounced maximum, while the recurrence of sunshine is frequently responsible for a second rise and sub-maximum (Experiments 2 and 3). The occurrence of a sub-maximum before the actual maximum of the day is rare. A slight increase of the evaporation rate in the early afternoon may be accompanied by a relatively pronounced increase of the transpiration, as occurred at 1 p. m. and 3 p. m. in Experiment 3. The later in the afternoon such secondary maxima of evaporation occur, the less is the response of the transpiration rate: such a

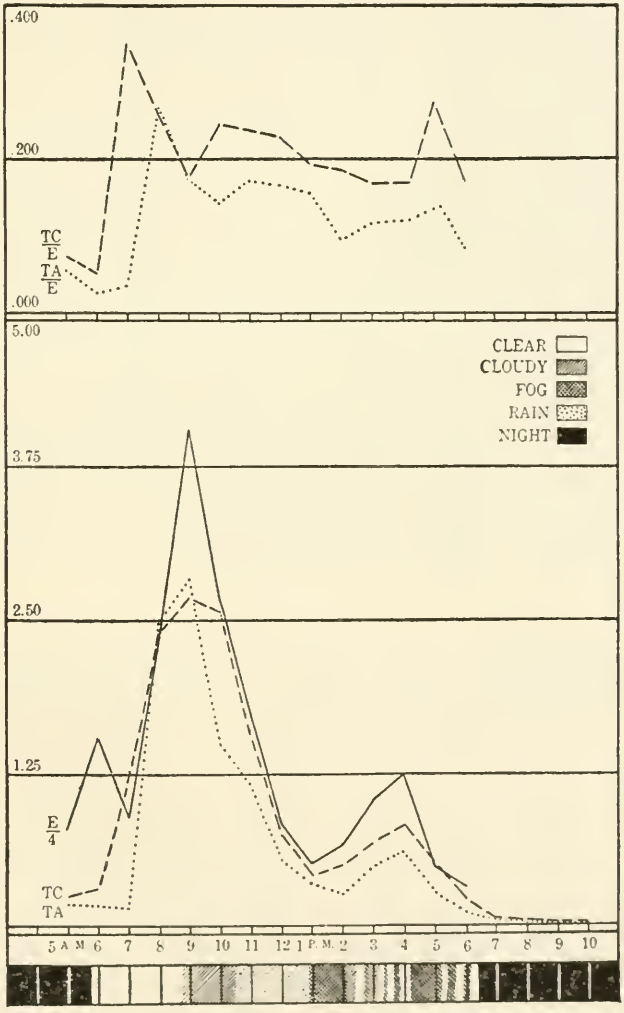


FIG. 2.—Daily march of transpiration in *Clethra* (TC) and *Alchornea* (TA), together with concurrent rate of evaporation $\left(\frac{E}{4}\right)$, rates of relative transpiration for the two plants, $\frac{TC}{E}$ and $\frac{TA}{E}$ respectively, and schematic depiction of weather conditions.

maximum in Experiment 3 at 6 p. m. affecting neither *Pilea* nor *Peperomia* (table 18, fig. 4); slight secondary maxima in Experiment 2 affecting *Dodonæa* slightly on the first day of the experiment and not at all on the

second; a secondary maximum in the late afternoon of the third day of Experiment 4, at 6 o'clock, having a positive effect on the rate of *Peperomia basellæfolia*, causing checks in the rate of fall of *Asplenium*, *Diplazium*, and *Peperomia turfosa*, and failing to affect *Pilea nigrescens*. Very pronounced rises of evaporation in the night are frequent at Cinchona because of the nocturnal winds, and these rises are frequently accompanied by slight increases of transpiration, as may be seen in the case of *Dodonæa* (Experiment 2, table 17, fig. 3) at 8 and 9 p. m., and in the case of five species under simultaneous investigation (Experiment 5, table 20, fig. 6) at midnight. The nocturnal rates of absolute transpiration, as compared with the diurnal, are not usually very low. An examination of the curves for five species run through the 24 hours (Experiment 5, table 20, fig. 6) shows that the lowest nocturnal readings were related to the highest diurnal readings as indicated by the following percentages: *Diplazium*, 44 per cent; *Asplenium*, 40 per cent; *Pilea*, 36 per cent; *Peperomia turfosa*, 20 per cent; *Peperomia basellæfolia*, 21 per cent. In Experiment 4 (table 19, fig. 5) the first reading taken in the morning on the first and third days of the experiment was an all-night reading, and its amount, determined at 6 a. m., may be compared with maximum rate for one day, which was abnormally low on the first day, but normal on the third. On tables 23, 24, and 25, the all-night readings of transpiration are indicated, and their amounts may be compared with the diurnal amounts for a number of experiments with three species, and about the same relation will be found to hold between nocturnal and diurnal rates as is indicated by the above percentages, although occasional very low nocturnal rates are registered.

TABLE 16.—*Transpiration of Clethra occidentalis and Alchornea latifolia.*

EXPERIMENT 1.—Series run in open air with severed shoots, by potometer method. Clethra, 9 leaves, area 234.5 sq. cm.; Alchornea, 13 leaves, area 376.9 sq. cm.

Day of month.	Hour.	Temperature.	Humidity.	Evaporation.	Clethra.		Alchornea.	
					T	$\frac{T}{E}$	T	$\frac{T}{E}$
Feb. 2....	4 a.m.	56	73	....	....	.....	.....	.....
	5	51	94	3.20	0.23	0.072	0.18	0.056
	6	55	70	6.20	.30	.048	.16	.026
	7	55	73	3.60	1.26	.351	.13	.036
	8	60	53	9.40	2.43	.257	2.48	.263
	9	62	67	16.20	2.78	.172	2.84	.175
	10	67	69	10.50	2.56	.244	1.48	.141
	11	59	90	6.80	1.59	.235	1.16	.171
	12 p.m.	60	90	3.30	.74	.226	.55	.166
	1	61	93	2.10	.40	.190	.34	.156
	2	60	92	2.70	.49	.182	.26	.096
	3	63	90	4.10	.67	.163	.49	.119
	4	59	92	4.90	.82	.168	.60	.121
	5	59	91	1.90	.51	.271	.27	.139
	6	58	90	1.30	.22	.169	.11	.085
	7	55	92	....	.06	....	.05	....
	8	55	91	....	.03	....	.02	....
	9	56	88	....	.02	....	.01	....
	10	55	89	1.20	.02	.012	.01	.008

TABLE 17.—*Transpiration of Dodonæa angustifolia.*

EXPERIMENT 2.—Series run in open air, excepting from 2 to 5 p. m., February 28, by weighing method. Plant had 43 leaves, area 147.9 sq. cm.

Day of month.	Hour.	Temperature.	Humidity.	Evaporation.	T	$\frac{T}{E}$
Feb. 27.....	9 p.m.	.....	.....	.....	.....	.....
Feb. 28 ...	6 a.m.	65	90	.....	0.11	.....
	7	68	80	.....	.20	.....
	8	64	61	4.30	1.35	0.314
	9	69	63	7.40	5.61	.758
	10	65	85	11.50	3.89	.338
	11	65	77	6.20	2.42	.390
	12 p.m.	66	80	3.60	2.64	.731
	1	65	78	.....	3.95	.....
	2	67	80	4.00	1.62	.405
	3	67	75	7.20	2.12	.291
	4	63	80	10.00	2.23	220
	5	59	90	6.90	1.24	.180
	6	57	70	6.50	1.00	.154
	7	57	42	13.00	1.02	.078
	8	56	40	22.60	1.62	.072
	9	57	52	24.50	1.48	.061
	10	55	60	15.10	.77	.050
Mar. 1.....	6 a.m.	56	88	6.77	.58	.085
	7	58	87	.....	.43	.....
	8	65	70	5.50	2.39	.435
	9	67	64	10.40	.....	.....
	10	64	54	12.90	9.42	.730
	11	74	48	17.70	11.08	.626
	12 p.m.	79	49	19.10	9.56	.500
	1	79	43	21.90	10.57	.482
	2	71	62	22.00	7.30	.331
	3	62	73	13.40	6.52	.486
	4	66	83	15.10	5.37	.355
	5	63	86	6.60	2.30	.348
	6	59	89	3.80	.51	.135
	7	59	93	2.30	.67	.293
	8	57	95	1.00	.....	.....

TABLE 18.—*Transpiration of Pilea nigrescens and Peperomia turfosa.*

EXPERIMENT 3.—Series run in laboratory, with potted plants, by weighing method. Areas: *Pilea*, 110.9 sq. cm.; *Peperomia*, 55.3 sq. cm.

Day of month.	Hour.	Temperature.	Humidity.	Evaporation.	Pilea.		Peperomia.	
					T	$\frac{T}{E}$	T	$\frac{T}{E}$
July 23 ...	9 p.m.	66	68	.....	.....	.....	.....	.....
July 24...	5 a.m.	61	88	7.68	0.57	0.075	0.31	0.040
	6	61	95	4.08	.31	.077	.36	.089
	7	62	96	4.08	.56	.138	.54	.133
	8	64	90	5.40	.65	.121	.72	.134
	9	69	79	6.60	.81	.123	1.31	.198
	10	73	71	11.64	1.49	.128	1.49	.127
	11	75	79	8.34	1.34	.161	1.24	.148
	12 p.m.	75	83	7.92	1.31	.165	1.24	.157
	1	74	85	8.46	1.44	.170	1.43	.168
	2	75	92	6.72	1.24	.184	.96	.144
	3	72	90	7.68	1.06	.138	1.13	.147
	4	70	93	5.88	.68	.116	.77	.130
	5	69	96	5.04	.67	.132	.39	.077
	6	66	98	5.88	.56	.096	.32	.053
	9	62	98	4.23	.43	.101	.22	.051

TABLE 19.—*Simultaneous transpiration of five species.*

(SET A.) EXPERIMENT 4.—Series run in laboratory, at three intervals, with potted plants, by weighing method. Areas: *Pilea*, 120.5 sq. cm.; *Peperomia turfosa*, 98.8 sq. cm.; *Peperomia basellæfolia*, 103.9 sq. cm.; *Diplazium*, 321.5 sq. cm.; *Asplenium*, 192.7 sq. cm.

Day of Month.	Hour.	Temperature.	Humidity.	Evaporation.	Pilea nigrescens.		Peperomia turfosa.		Peperomia basellæfolia.		Diplazium celtidifolium.		Asplenium alatum.	
					T	$\frac{T}{E}$	T	$\frac{T}{E}$	T	$\frac{T}{E}$	T	$\frac{T}{E}$	T	$\frac{T}{E}$
Oct. 6.	9 p.m.....	..	..	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....
Oct. 7.	6 a.m.....	60	95	5.23	0.19	0.037	0.17	0.033	0.09	0.018	0.52	0.099	0.58	0.112
	9	62	96	3.40	.25	.074	.27	.079	.16	.047	.37	.109	.53	.156
	12 p.m.....	63	92	3.40	.41	.119	.39	.116	.18	.052	.53	.156	.73	.214
	3	62	95	4.07	.36	.088	.38	.093	.20	.049	.45	.112	.63	.156
	6	61	95	6.23	.42	.067	.33	.052	.17	.027	.56	.090	.80	.128
Oct. 11.	7 a.m.....	63	92	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....
	9	70	89	3.07	.34	.111	.21	.068	.18	.059	.52	.169	.84	.274
	11	73	83	12.00	.76	.051	.76	.062	.58	.048	1.12	.093	1.56	.129
	1 p.m.....	72	83	16.12	1.09	.067	.92	.057	.67	.041	1.43	.089	1.81	.112
	3	69	89	15.52	1.03	.066	.87	.056	.48	.031	1.25	.080	1.56	.101
	5	67	90	11.02	.57	.052	.50	.046	.25	.023	.87	.079	1.23	.112
	7	64	93	5.85	.26	.044	.15	.026	.20	.035	.44	.076	.64	.109
	9	63	92	4.27	.19	.045	.32	.074	.17	.039	.42	.097	.63	.147
Oct. 15.	$9^h\ 30^m$ p.m.	..	..	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....
Oct. 16.	6 a.m.....	..	..	6.36	.23	.036	.21	.033	.23	.035	.70	.111	1.02	.160
	8	..	..	4.50	.19	.042	.13	.028	.06	.014	.42	.094	.66	.147
	10	..	..	11.77	.79	.067	.77	.066	.56	.047	1.17	.099	1.43	.122
	12 p.m.....	..	..	23.01	1.58	.068	1.48	.064	1.25	.054	2.32	.100	2.41	.105
	2	..	..	16.20	1.05	.064	.78	.048	.61	.038	1.56	.098	1.92	.118
	4	..	..	13.95	.73	.052	.39	.028	.24	.017	1.01	.072	1.30	.093
	6	..	..	16.72	.33	.019	.37	.022	.32	.019	.93	.055	1.15	.068
	9	..	..	7.80	.19	.024	.10	.013	.13	.017	.64	.082	.86	.111
Oct. 17.	8 a.m.....	..	..	8.52	.18	.020	.14	.017	.12	.014	.54	.063	.73	.086

TABLE 20.—*Simultaneous transpiration of five species.*

(SET B.) EXPERIMENT 5.—Series run in laboratory with potted plants, by weighing method. Areas: *Pilea*, 106.0 sq. cm.; *Peperomia turfosa*, 113.6 sq. cm.; *Peperomia basellæfolia*, 113.3 sq. cm.; *Diplazium*, 220.0 sq. cm.; *Asplenium*;, 380.8 sq. cm.

Day of month.	Hour.	Evaporation.	Pilea nigrescens.		Peperomia turfosa.		Peperomia basellæfolia.		Diplazium celtidifolium.		Asplenium alatum.	
			T	$\frac{T}{E}$	T	$\frac{T}{E}$	T	$\frac{T}{E}$	T	$\frac{T}{E}$	T	$\frac{T}{E}$
Oct. 29.....	6 p.m.	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....
	8	8.55	0.51	0.059	0.22	0.026	0.27	0.032	1.01	0.117	0.81	0.094
	10	7.80	.39	.049	.25	.032	.21	.027	1.03	.132	.86	.110
Oct. 30.....	12 a.m.	9.45	.42	.044	.24	.026	.24	.025	1.27	.134	1.08	.114
	2	7.95	.29	.037	.31	.038	.21	.027	1.13	.142	.94	.118
	4	7.05	.28	.040	.22	.031	.17	.024	.99	.141	.88	.127
	6	8.32	.33	.039	.34	.041	.15	.018	1.14	.136	.91	.109
	8	8.47	.38	.044	.51	.059	.36	.043	1.32	.156	1.16	.137
	10	10.05	.62	.062	.99	.098	.72	.072	1.99	.197	1.71	.170
	12 p.m.	11.92	.74	.066	1.14	.095	.61	.051	2.25	.189	1.99	.167
	2	7.72	.46	.059	.53	.068	.22	.029	1.17	.151	.91	.118
	4	6.00	.47	.078	.29	.047	.15	.025	.91	.152	.94	.156
	6	7.05	.41	.059	.46	.065	.21	.029	.97	.136	.80	.113
Oct. 31.....	8 a.m.	4.09	.20	.049	.20	.050	.11	.026	.56	.136	.53	.130
	10	6.60	.64	.096	.74	.112	.62	.094	1.53	.232	1.52	.230
	12 p.m.	9.97	.82	.082	.88	.088	.48	.047	1.70	.170	1.65	.082
	2	6.82	.47	.069	.48	.070	.13	.019	.97	.142	.94	.251
	4	7.35	.49	.067	.52	.070	.21	.029	1.18	.160	1.13	.154
	6	6.97	.52	.074	.51	.072	.21	.030	.86	.123	.92	.132

Inasmuch as the absolute transpiration rate is of minor significance when considered independently of the concurrent rate of evaporation, the entire subject of the amplitude of the fluctuations of transpiration in each species, and the comparative rates of different species, will be taken up in the discussion of their relative transpiration rates. Suffice it to give here some of the extremes of absolute transpiration, considered entirely apart from the rates of evaporation by which they were accompanied (table 21).

TABLE 21.—*Extreme rates of absolute transpiration for unit time and area.*

Milligrams per hour per square centimeter.

Plant.	Maximum.	Minimum.
	mg.	*mg.*
Clethra occidentalis	2.78	0.02
Alchornea latifolia	2.84	.01
Dodonæa angustifolia	11.08	.11
Pilea nigrescens	1.58	.10
Peperomia turfosa	1.75	.10
Peperomia basellæfolia	1.25	.06
Diplazium celtidifolium	5.11	.37
Asplenium alatum	2.41	.53

TABLE 22.—*Comparative rates of transpiration and relative transpiration in five species.*

Transpiration amounts are the average hourly loss per square centimeter for the number of readings stated.

Plants.	No. of readings.	Duration of readings.	Total evaporation.	Pilea nigrescens.	Peperomia turfosa.	Peperomia basellæfolia.	Diplazium celtidifolium.	Asplenium alatum.
Set A	5	6 a.m. to 6 p.m.	4.465	0.324	0.308	0.160	0.488	0.655
Set A	7	9 a.m. to 9 p.m.	9.696	.605	.533	.362	.866	1.182
Set A	9	6 a.m. to 9 p.m.; 8 a.m.	12.093	.584	.485	.393	1.038	1.278
Set A	Averages		8.751	.504	.442	.305	.797	1.038
Set B	5	8 p.m. to 4 a.m.	8.160	.379	.248	.223	1.085	.915
Set B	7	6 a.m. to 6 p.m.	8.507	.495	.608	.347	1.394	1.205
Set B	6	8 a.m. to 6 p.m.	6.969	.525	.555	.295	1.134	1.117
Set B	Averages		7.879	.466	.470	.288	1.204	1.079
Averages of Sets A and B			8.315	.485	.456	.296	1.001	1.059
Set A				.077	.074	.038	.113	.153
Set A				.063	.056	.039	.098	.141
Set A				.044	.036	.029	.087	.113
Set A	Averages			.061	.055	.035	.099	.136
Set B				.046	.030	.027	.133	.113
Set B				.058	.068	.038	.160	.138
Set B				.073	.077	.041	.161	.164
Set B	Averages			.059	.058	.035	.151	.138
Averages of Sets A and B				.060	.056	.035	.125	.137

TABLE 23.—*Amounts of transpiration and relative transpiration in Pilea nigrescens.*

Values given are for eight sets of readings, all secured in laboratory by weighing method. Each individual plant is designated by letter. Starred readings are for intervals extending through the night.

Hours.	July 24.		Aug. 6.						Aug. 7.		Sept. 18.			
	Plant A.		Plant A.		Plant B.		Plant C.		Plant B.		Plant D.		Plant E.	
	T	T/E	T	T/E	T	T/E	T	T/E	T	T/E	T	T/E	T	T/E
5 a.m.	*0.57	0.075												
6	.31	.077	*0.22	0.113	*0.10	0.049	*0.08	0.041						
7	.56	.138												
8	.65	.121	.29	.195	.21	.143	.10	.071	0.130	0.182				
9	.81	.123												
10	1.49	.128	.65	.213	.44	.143	.42	.136	.30	.208	*0.10	0.080	*0.16	0.124
11	1.34	.161												
12 p.m.	1.31	.165	.68	.184	.49	.131	.29	.078	.62	.207	1.08	.107	1.35	.133
1	1.44	.170												
2	1.24	.184	1.28	.196	.86	.132	.49	.074	.44	.175	1.08	.070	1.49	.097
3	1.06	.138												
4	.68	.116	.68	.172	.37	.094	.35	.088	.35	.188	.67	.071	.86	.098
5	.67	.132												
6	.56	.096	.45	.141	.28	.091	.17	.052	.27	.109				
7											.64	.063	.88	.087
8			.45	.122	.24	.067	.22	.060						
9	.43	.101							.28	.069				

Hours.	Oct. 11.		Oct. 16.		Oct. 30.		Oct. 31.		Averages of T/E	
	Plant F.		Plant F.		Plant G.		Plant G.			
	T	T/E	T	T/E	T	T/E	T	T/E		
5 a. m.										
6			*0.23	0.036	0.33	0.039			Night:*	0.071
7										
8			.19	.041	.38	.045	*0.20	0.050	8– 9:	.116
9	0.34	0.111								
10			.79	.067	.62	.062	.64	.096	10–11:	.126
11	.75	.051								
12 p. m.			1.58	.068	.79	.066	.82	.082	12– 1:	.121
1	1.09	.067								
2			1.05	.064	.46	.059	.47	.069	2– 3:	.110
3	1.03	.066								
4			.73	.052	.47	.078	.49	.067	4– 5:	.101
5	.57	.051								
6			.33	.020	.41	.058	.52	.075	6– 7:	.076
7	.26	.044								
8									8– 9:	.070
9	.19	.045	.19	.024						

TABLE 24.—*Amounts of transpiration and relative transpiration in Peperomia turfosa.*

Values given are for eight sets of readings, all secured in laboratory by weighing method. Each individual plant is designated by letter. Starred readings are for intervals extending over night.

Hours.	July 24.		July 31.		Oct. 7.		Oct. 11.		Oct. 16.		Oct. 22.					
	Plant A.		Plant A.		Plant B.		Plant B.		Plant B.		Plant C.		Plant D.		Plant E.	
	T	T/E	T	T/E	T	T/E	T	T/E	T	T/E	T	T/E	T	T/E	T	T/E
5 a.m.	*0.310	0.040														
6	.36	.089	*0.310	0.044	*0.170	0.033			*0.210	0.033						
7	.54	.133									*0.290	0.058	*0.330	0.067	*0.370	0.075
8	.72	.134	.23	.069					.13	.028						
9	1.31	.198			.27	.080	0.210	0.068			.65	.105	.66	.106	.88	.141
10	1.49	.127	.74	.114					.77	.066						
11	1.24	.148					.76	.063								
12 p.m.	1.24	.157	.74	.118	.39	.116			1.48	.064	.57	.106	.43	.079	.66	.122
1	1.43	.168					.92	.057								
2	.96	.144	.97	.131					.78	.049						
3	1.13	.147			.38	.093	.87	.056			.20	.067	.35	.118	.36	.121
4	.77	.130							.39	.028						
5	.39	.077					.50	.046								
6	.32	.053			.33	.052			.37	.022	.30	.092	.26	.079	.30	.092
7							.15	.026								
8																
9	.22	.051					.31	.074	.10	.013						

Hours.	Oct. 23.						Oct. 24.						Averages of T/E	
	Plant C.		Plant D.		Plant E.		Plant C.		Plant D.		Plant E.			
	T	T/E	T	T/E	T	T/E	T	T/E	T	T/E	T	T/E		
5 a. m.													Night:*	0.067
6														
7														
8													8– 9:	.086
9	*0.250	0.078	*0.290	0.092	*0.270	0.085	*0.150	0.088	*0.140	0.087	*0.150	0.090		
10													10–11:	.081
11														
12 p. m.	.75	.102	.56	.075	.83	.113	1.71	.106	1.30	.080	1.75	.108	12– 1:	.096
1														
2													2– 3:	.086
3	.51	.082	.45	.072	.67	.108	.97	.072	.78	.058	1.25	.093		
4													4– 5:	.037
5														
6	.33	.070	.36	.077	.40	.086	.38	.041	.26	.028	.65	.071	6– 7:	.061
7														
8													8– 9:	.044
9							.48	.078	.17	.027	.18	.028		

TABLE 25.—*Amounts of transpiration and relative transpiration in Diplazium celtidifolium.*

Values are given for seven sets of readings, all secured in laboratory by weighing method. Each individual plant is designated by letter. Starred readings are for intervals extending over night.

Hours.	Oct. 7.		Oct. 11.		Oct. 16.		Oct. 30.		Oct. 31.	
	Plant A.		Plant A.		Plant A.		Plant B.		Plant B.	
	T	$\frac{T}{E}$	T	$\frac{T}{E}$	T	$\frac{T}{E}$	T	$\frac{T}{E}$	T	$\frac{T}{E}$
5 a.m.										
6	*0.52	0.099			*0.70	0.111	1.14	0.136		
7										
8					.42	.094	1.32	.156	*0.56	0.136
9	.37	.109	0.52	0.169						
10					1.17	.099	1.99	.197	1.53	.232
11			1.12	.093						
12 p.m.	.53	.156			2.32	.100	2.25	.189	1.70	.170
1			1.43	.089						
2					1.60	.098	1.17	.151	.97	.142
3	.45	.111	1.25	.080						
4					1.01	.072	.91	.152	1.18	.161
5			.87	.079						
6	.56	.090			.93	.055	.97	.136	.86	.123
7			.44	.076						
8										
9			.41	.097	.64	.082				

Hours.	Nov. 19.						Nov. 20.						Averages of $\frac{T}{E}$
	Plant C.		Plant D.		Plant E.		Plant C.		Plant D.		Plant E.		
	T	$\frac{T}{E}$	T	$\frac{T}{E}$	T	$\frac{T}{E}$	T	$\frac{T}{E}$	T	$\frac{T}{E}$	T	$\frac{T}{E}$	
5 a.m.													
6													Night*: 0.115
7													
8													
9	*1.12	0.125	*1.22	0.137			*0.79	0.149	*0.90	0.169	*1.25	0.234	8– 9: .148
10													
11	2.12	.152	2.38	.171			2.68	.171	2.81	.179	3.46	.221	10–11: .168
12 p.m.													
1	3.33	.142	3.74	.158			3.60	.144	4.14	.165	5.11	.204	12– 1: .152
2													
3	3.22	.154	3.43	.164	4.18	0.200							2– 3: .137
4													
5													4– 5: .116
6	1.76	.131	1.64	.122	2.48	.184							6– 7: .115
7													
8													9: .089
9													

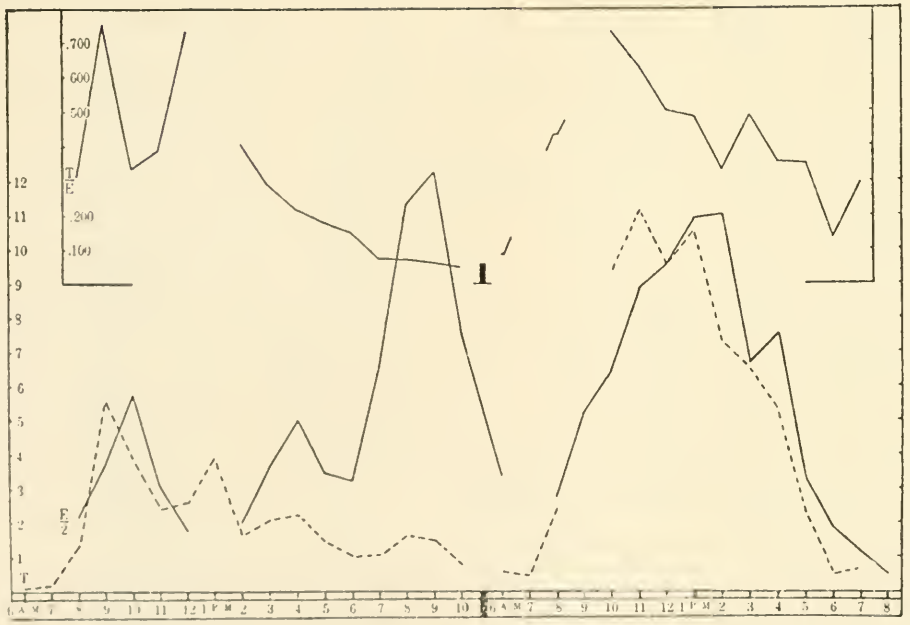


FIG. 3.—Daily march of transpiration (T) in *Dodonæa* for two days with concurrent evaporation $\left(\frac{E}{2}\right)$, and partial curve of relative transpiration $\left(\frac{T}{E}\right)$.

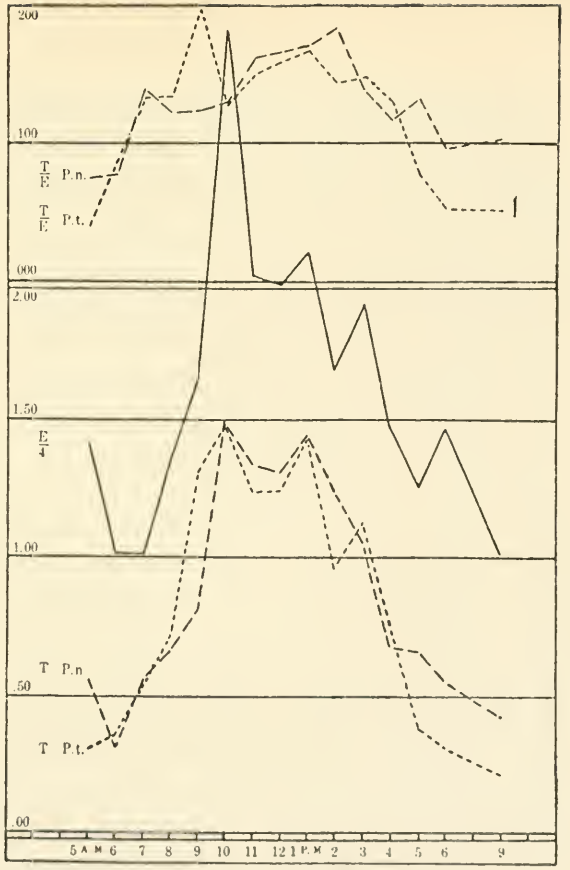


FIG. 4.—Daily march of transpiration in *Pilea nigrescens* (T. P. n.) *Peperomia turfosa* (T P. t.), together with march of evaporation $\left(\frac{E}{4}\right)$ and curves of relative transpiration for the two plants, $\frac{T}{E}$ P. n. and $\frac{T}{E}$ P. t. respectively.

INDIVIDUAL VARIABILITY OF TRANSPIRATION RATE.

Several experiments were performed which gave simultaneous readings of the transpiration of two or three individuals of the same species. In each case the individual plants used were from the same spot in the rain-forest, were potted at the same time, and in every respect treated in the same manner up to the time of experimentation. The uniformity of soil-moisture conditions in the pots of the plants which I used for experimentation has already been mentioned. In spite of the apparent equivalency of the plants, and the fact that they stood side by side during the experiments, the rates of transpiration, *when reduced to comparable areas*, were found to differ to a considerable extent. On August 6 three plants of *Pilea nigrescens* were run in parallel series and readings of their transpiration were taken simultaneously. The plants were designated A, B, and C (see table 23) and their leaf areas were respectively 222 sq. cm., 326 sq. cm., and 360 sq. cm. On adding the hourly quantities of transpiration per square centimeter shown in table 23 the following totals are secured for the eight readings: A, 4.70 mg.; B, 2.99 mg.; C, 2.12 mg.

On September 18 two plants of *Pilea*, D and E, were run simultaneously (see table 23), and their areas were determined as: D, 427 sq. cm.; E, 205 sq. cm. The total of the hourly quantities of transpiration, per unit area, for these plants is: D, 3.57; E, 4.74.

On October 22, 23, and 24 three plants of *Peperomia turfosa* were run simultaneously. Their leaf areas and collective transpiration amounts per unit area are shown in table 26.

TABLE 26.

	Plant C.	Plant D.	Plant E.
Area (in sq. cm.)	167	129	227
Transpiration, October 22	2.01	2.03	2.57
Transpiration, October 23	1.84	1.66	2.17
Transpiration, October 24	3.21	2.48	3.80

On November 19 and 20 plants of *Diplazium celtidifolium* (see table 25) were run simultaneously, and the areas of leaf surface and the total transpiration amounts per unit area were as follows:

TABLE 27.

	Plant C.	Plant D.	Plant E.
Area (in sq. cm.)	445	454	363
Transpiration, November 19	11.55	12.41	....
Transpiration, November 20	7.07	7.85	9.82

The figures given for the three species indicate that all of them show variability in the amounts of their transpiration, sometimes slight, sometimes considerable. The fact that the plants in each series were placed side by side during the determination of their transpiration amounts, and were therefore under identical atmospheric conditions, together with the fact that the soil character and soil moisture were so nearly identical as to be incapable of exerting an influence on the available water supply, points to internal, physiological factors as causing the differences. There is evidence in the cases of *Pilea* and *Diplazium* that the plants which have smaller leaf area have higher transpiration totals, indicating a greater transpiration activity on the part of the smaller and younger plants. For *Peperomia*, however, these relations are reversed, at least on the second and third days, two plants of different area having almost identical totals on the first day.

Such differences of behavior between plants of the same species under such nearly identical conditions is probably true of very many functions other than the transpiration. A row of plants grown in greenhouse or garden from the same seed, planted at the same time, with identical water supply and soil, will grow at different rates. Differences in growth rate and other activities may often be observed in plants growing in their natural environment, although in the field it is always more difficult to be assured that the environmental conditions are so nearly equal as under glass or in the garden. Such differences of individual activity are an index of differences in the character or intensity of the many functions being performed by the plant, and may well be correlated with such differences in individual functions as have been shown to be true transpiration. There is apparently no definite specific rate of transpiration for the rain-forest plants investigated, although each species fluctuates around a normal rate for a given set of conditions and the limits of variability are different for different species.

CONCURRENT RATES OF TRANSPIRATION IN DIFFERENT SPECIES.

Several experiments were performed in which five plants of different species were run concurrently, with a view to ascertaining the degree of similarity or difference in their transpiration behavior under the same atmospheric conditions and to comparing the amounts of water loss from the different species; also, in view of the individual variability of transpiration, to discover any possible changes in the relation of the species to each other as respects transpiration amount, in different series of the same sort. The species used for these experiments were *Pilea nigrescens*, *Peperomia turfosa*, *Peperomia basellæfolia*, *Diplazium celtidifolium*, and *Asplenium alatum*, the habitat differences of which have already been mentioned. Two sets of the five species were used. The entire series of readings for Set A is shown in table 19, those for Set B in table 20 (see figs. 5 and 6).

An examination of the curves in figure 5 will give a graphic conception of the comparative behavior of the five species in Set A, on three non-consecutive days, with progressively increasing evaporation. The curves for the five plants are such as to reveal the dominant influence of evaporation rate in controlling the transpiration. The water loss of *Asplenium alatum* tended to exceed one-tenth of the evaporation, area for area, throughout the three days, but exceeded it the least on the day possessing the highest evaporation. *Diplazium celtidifolium* ran considerably below one-tenth of the evaporation on the second day,

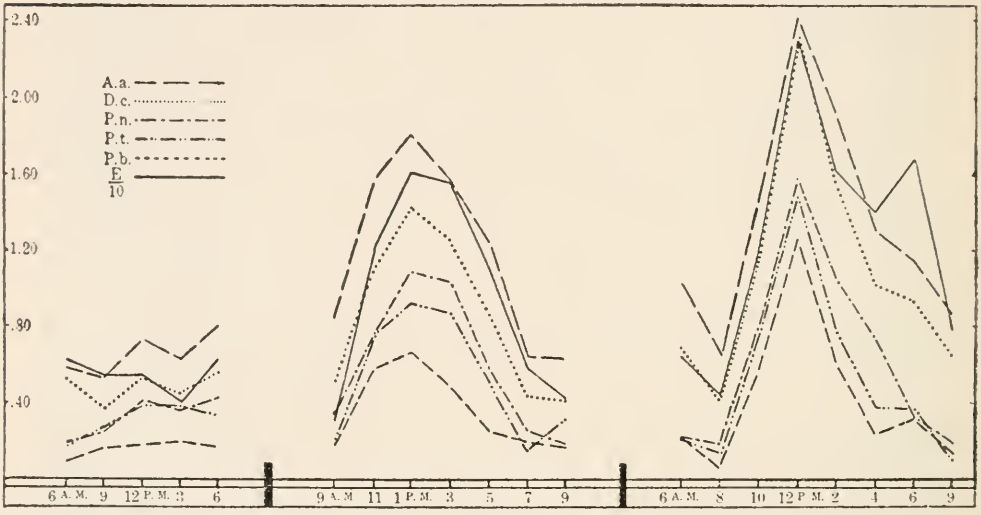


FIG. 5.—March of evaporation and of transpiration for five species during three days. The species are: *Asplenium alatum* (A. a.), *Diplazium celtidifolium* (D. c.), *Pilea nigrescens* (P. n.), *Peperomia turfosa* (P. t.), and *Peperomia basellæfolia* (P. b.). Evaporation is plotted at one-tenth its scale value.

but parallel it closely on the third, indicating that it is capable of withstanding an evaporation of 23 mg. per sq. cm. per hour—the rate at 12 noon on the third day—without evidence of wilting. The three species of lower transpiring rate than the ferns show a behavior in which they sustain approximately the same relation to each other during the three days, except for the tendency of the plants of lowest transpiring power to exhibit a relatively more rapid rate of increase with increasing evaporation. It is particularly true of *Peperomia basellæfolia* that its rate of water-loss gradually approaches that of *Peperomia turfosa* on each of the successsive days.

In the curves of figure 6 is exhibited the behavior of Set B of the five species under discussion. The evaporation runs slightly lower in this experiment than on the second day of the running of Set A, and the transpiration of *Diplazium* and *Asplenium* outruns one-tenth of it. The close correlation of the rates for all five of the plants with the rate of evaporation is quite as marked as in the case of Set A. The relation

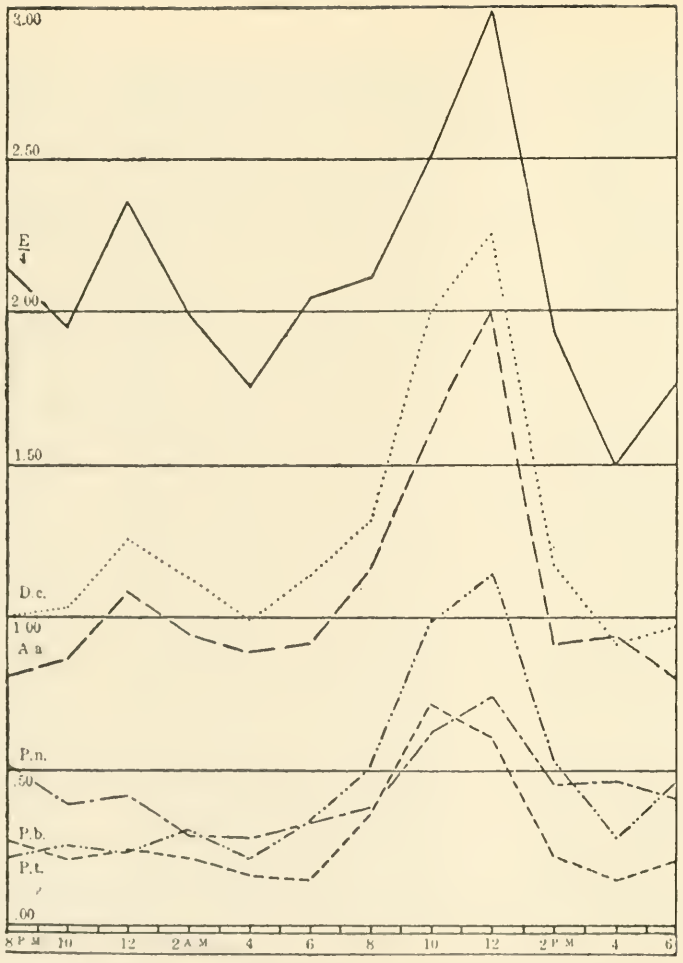


FIG. 6.—March of evaporation and of transpiration for five species (see fig. 5) through a 24-hour period.

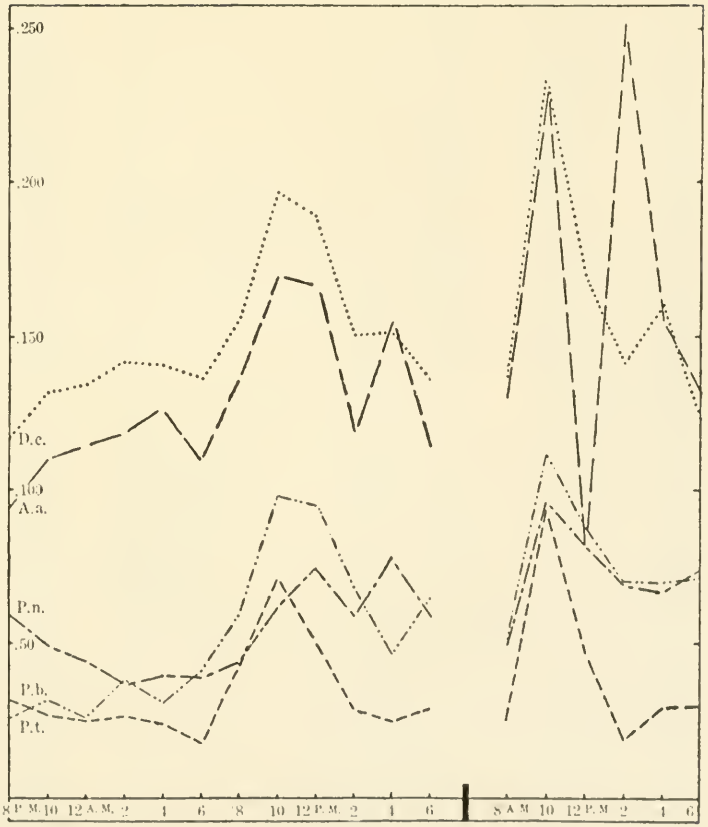


FIG. 7.—Curves of relative transpiration rate for the five species, covering the 24-hour period for which transpiration readings are given in figure 6 and succeeding day.

of *Asplenium* and *Diplazium* with reference to each other is reversed, but the remaining species sustain about the same relation to each other and to the two ferns as in the preceding series.

In table 22 are given the average hourly amounts of transpiration for the five species, for each experiment with Set A and Set B. The nocturnal readings of Set B shown in figure 6 are separated from those of the following day in this table.

When the averaged readings of transpiration for the five species, during a series of periods in which all was subjected to the same evaporation conditions, are compared on the basis of the rate of the lowest one as unity, the following figures are secured, which may be designated the coefficients of transpiring power:

TABLE 28.

Species.	Coefficient.
Peperomia basellæfolia	1.00
Peperomia turfosa	1.54
Pilea nigrescens	1.64
Diplazium celtidifolium	3.38
Asplenium alatum	3.57

A close relation is here brought out between the character of the habitats occupied by these species and their coefficients of transpiring power. *Peperomia basellæfolia* is a plant of the xerophilous ridges, or a mid-height epiphyte, while *Peperomia turfosa* and *Pilea nigrescens* are found in the Slope and open Ravine forests, and *Diplazium* and *Asplenium* only in the most hygrophilous of the Windward Ravines (see coefficients for moist chamber, p. 104).

RELATIVE TRANSPIRATION.

The securing of the rate of evaporation concurrently with all transpiration readings has made possible the determination of the rate of relative transpiration—the ratio of transpiration to evaporation. The ratios are determined by dividing the transpiration, in terms of the loss per hour per square centimeter of leaf surface, into the evaporation per square centimeter per hour from a free water surface. The transmutation of the atmometric readings of evaporation into terms of free water surface has been described on page 46. The relative transpiration figures are a true index of the transpiration rate as determined by the internal or physiological conditions of the plant and by the influence of light, in so far as its effects on the plant and the atmometer are different. The fact that all work here reported was done in the shade—in conformity with the conditions of the rain-forest—makes the error of relative transpiration figures due to light effects less than it would be in the case of experiments performed partly in the shade and partly

in the sun, as would be the case under the natural conditions of the open. The figures for relative transpiration not only serve as an index of the changing physiological conditions of the plant (fluctuations of stomatal aperture, of water content of leaf, of vascular transfer of water, conditions of soil moisture, etc.), but they also make possible a strict comparison of the behavior of a species when investigated on different days.

The usual daily course of the relative transpiration in all of the species investigated shows an early morning rise to a maximum which is earlier than the maximum of evaporation or that of transpiration and is usually the maximum of the relative rate for the entire day. In case the evaporation runs on to its maximum at a later hour than the maximum transpiration, or in case the two maxima coincide, it quite commonly happens that the relative rate reaches its maximum at an earlier hour than either. The fact that the rates of increase in evaporation and transpiration preceding their maximal points have been such that the rate of rise was greater for evaporation than the transpiration, causes a fall in the relative rate. Such fall is quite commonly followed in a few hours by a recovery, due to a pronounced fall in evaporation rate, accompanied by a less fall, of perhaps a rise, in the transpiration rate. The relative transpiration fluctuates during the mid-day and early afternoon in an irregular manner, sometimes reaching its daily maximum after the noon hour, but more commonly fluctuating below its morning maximum and finally falling in the late afternoon. The behavior of the rates for *Alchornea* and *Clethra* (table 16, fig. 2) is typical for a large number of cases investigated on normal days. The curves for *Pilea nigrescens* and *Peperomia turfosa* (table 18, fig. 4) show an even greater amount of mid-day fluctuation, and at 2 p. m. the former plant exhibits a maximum well above its early maximal point at 7 a. m.

Figures 8, 9, and 10 have been drawn to show the character of the daily relative transpiration curves in several experiments with *Pilea nigrescens*, *Peperomia turfosa*, and *Diplazium celtidifolium* respectively. Each individual plant used in more than one series is designated by the same letter throughout. The actual rates upon which these curves are drawn may be found in tables 23, 24, and 25. The relative rates of all three of these characteristic rain-forest herbaceous plants are characterized by their uniformity, indicating a weak operation of the physiological regulations to which the inconstancy of the relative rate must be attributed. The maximum and minimum relative rates of these three species are shown in table 29.

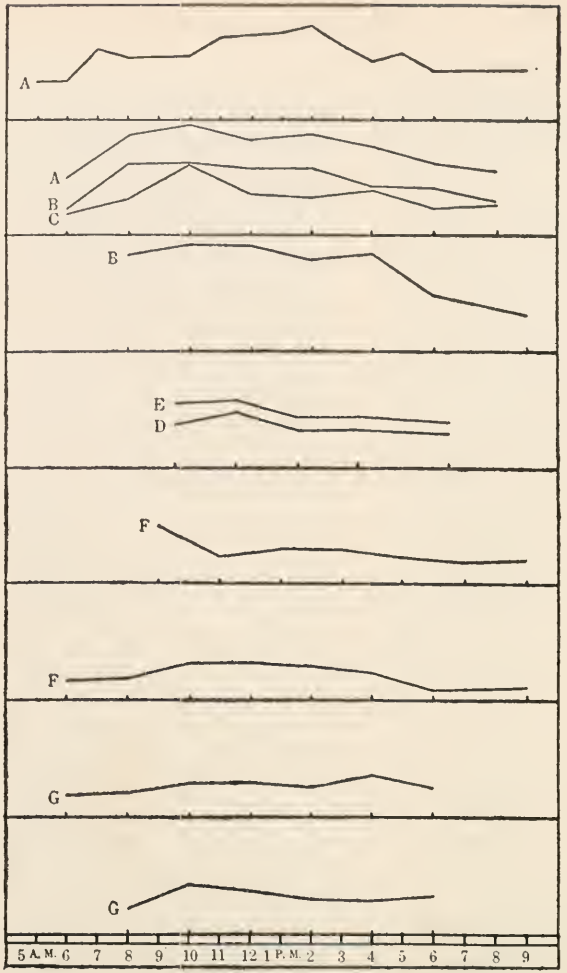


FIG. 8.—Relative transpiration graphs for successive experiments with *Pilea nigrescens*. Each individual plant used is designated by the same letter throughout. (For values see table 16.)

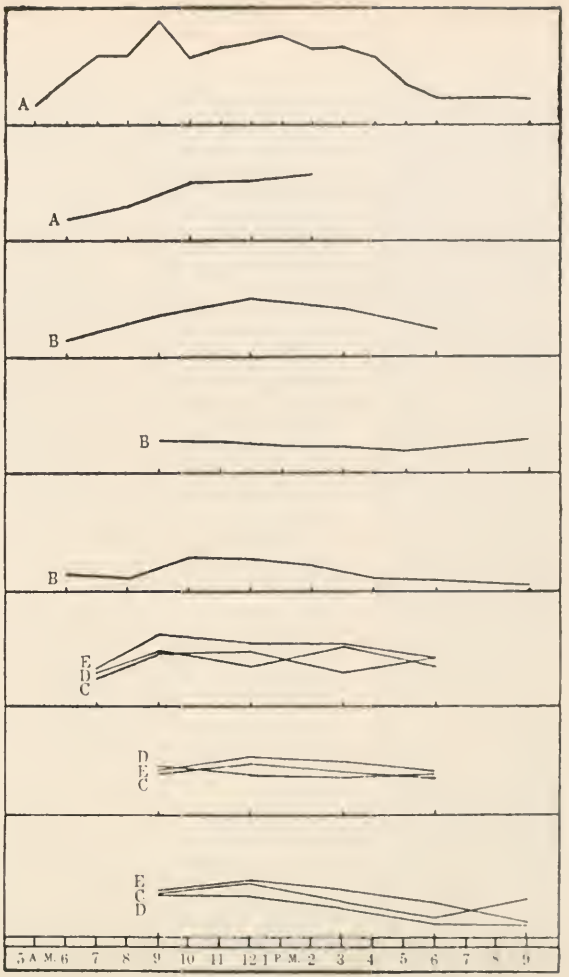


FIG. 9.—Relative transpiration graphs for successive experiments with *Peperomia turfosa*. Each individual plant used is designated by the same letter throughout. (For values see table 17.)

In table 29 and fig. 11 are shown the mean daily relative transpiration curves of *Pilea nigrescens*, *Peperomia turfosa*, and *Diplazium celtidifolium*, as determined respectively from the 84, 82, and 54 readings of tables 23, 24, and 25. There is a general similarity in the three curves,

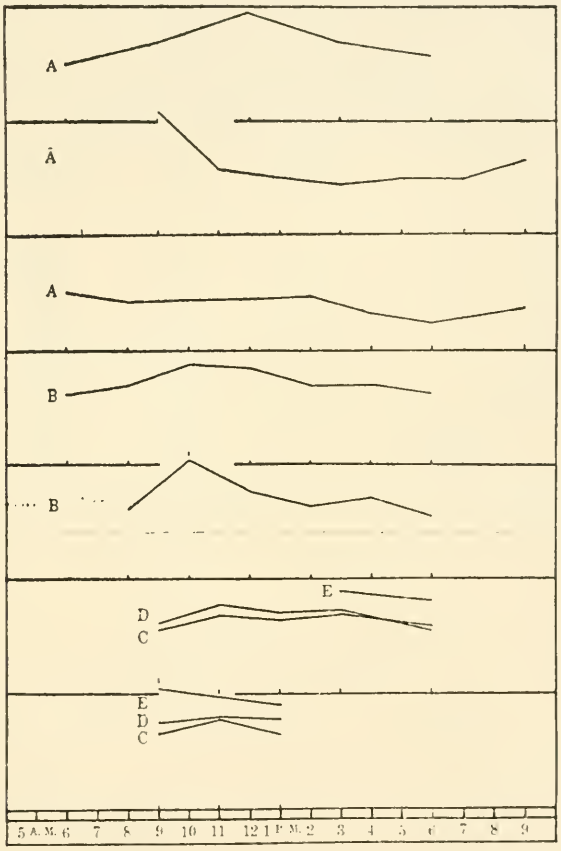


FIG. 10.—Relative transpiration graphs for successive experiments with *Diplazium celtidifolium*. Each individual plant used is designated by the same letter throughout. (For values see table 18.)

save for the tardy maximum of *Peperomia* and its low rate at the 4 p. m. and 5 p. m. readings. The rise of *Diplazium* at the 8 p. m. and 9 p. m. readings will be commented on later, in connection with its stomatal behavior. It may be observed here that the nocturnal relative rates are in no case as low as the lowest of the diurnal rates.

Inasmuch as several of the experiments show that there is a "break" in the morning rise of relative transpiration, before the hour at which the maximum evaporation of the day is recorded, an indirect method was employed to determine whether a progressive increase of evaporation rate is attended by a definite behavior on the part of the relative

transpiration. This was done in the following manner: The relative rates for the three plants exhibited in tables 23, 24, and 25 were grouped according to the rates of evaporation which prevailed during the same hours for which the relative rates were determined, and were grouped by increments of 1 milligram per square centimeter of water surface

TABLE 29.—*Averaged daily march of relative transpiration in three species, together with maximum and minimum readings.*

Averaged from 82 readings for *Peperomia turfosa*, 84 for *Pilea nigrescens*, and 56 for *Diplazium celtidifolium*.

Time of day.	Peperomia turfosa.	Pilea nigrescens.	Diplazium celtidifolium.
8 to 9 a.m.....	0.086	0.116	0.148
10 11	.081	.126	.168
12 1 p.m.....	.096	.121	.152
2 3	.086	.110	.137
4 5	.037	.101	.116
6 7	.061	.076	.115
8 9	.044	.070	.089
Night.....	.067	.071	.115
Maximum...	.198	.213	.234
Minimum....	.013	.020	.055

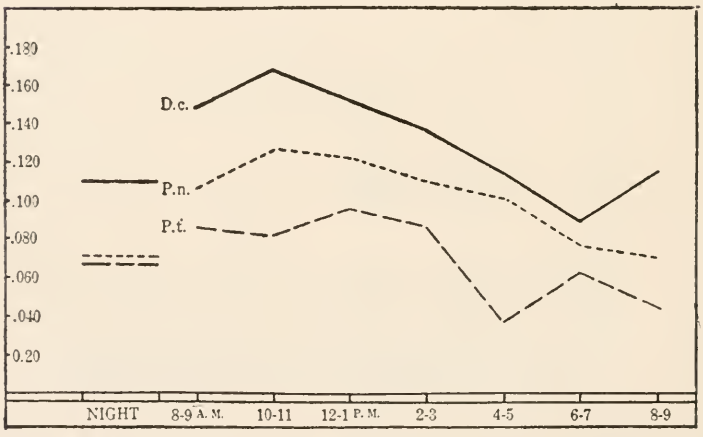


FIG. 11.—Mean daily course of relative transpiration rate for *Diplazium*, *Pilea*, and *Peperomia turfosa*, as averaged from graphs given in figs. 8, 9, and 10.

per hour. The averaged relative rates were then plotted to evaporation. The resulting curves show the collective behavior of the several plants experimented upon, in the several series in which they were run. On account of the many fluctuations of the curves they were smoothed in groups of three, the average of each three readings being taken as the value of the middle one of the three. The smoothed curves are given as dotted lines in figure 12. *Pilea* shows a fall in relative rate which is irregular but progressive; *Peperomia* shows a remarkable rise,

followed by an abrupt fall, but the general trend of the smoothed curve is downward; *Diplazium* exhibits irregular behavior, but its smoothed curve also shows a slight tendency to drop. The number of readings on which the placing of the points in these curves is based may be seen in table 30 to be small in many cases. A very much larger number of readings of relative transpiration, under varying conditions of evaporation, would make possible the construction of curves much more nearly representative of the actual influence exerted by a rising evaporation rate upon the physiological controls of the leaf and plant. The

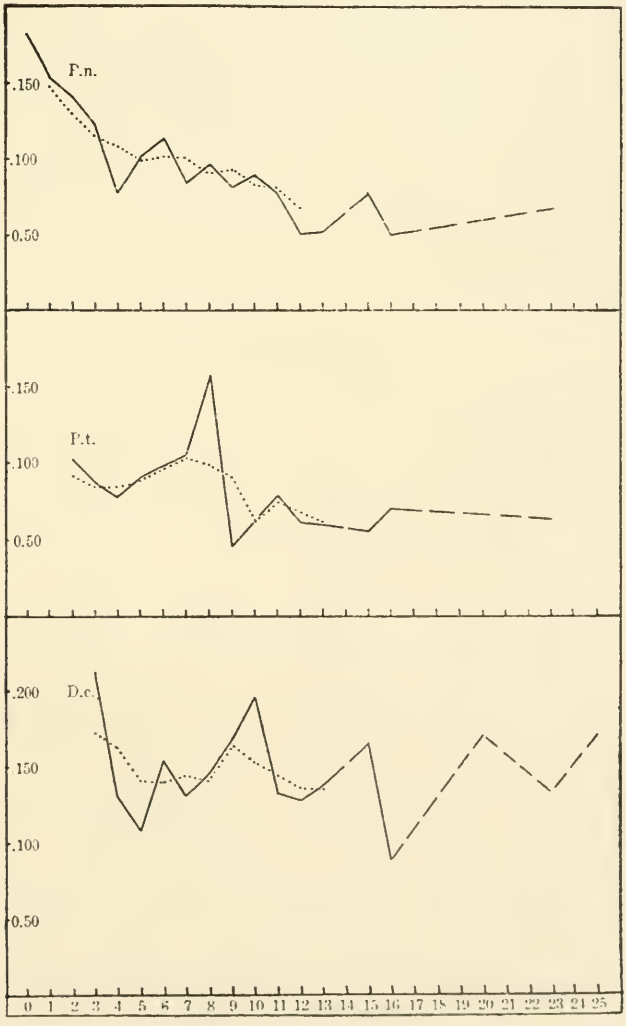


FIG. 12.—Graphs to show effect exerted upon relative transpiration rate by progressive increase of evaporation rate. Data secured for *Pilea*, *Peperomia turfosa*, and *Diplazium* (see tables 16, 17, and 18). Dotted lines are smoothed values.

curves under discussion show a slight general tendency toward a fall of relative rate with rising evaporation, but they fail to show a decided break in the relative rate, unless the abrupt rise and fall of *Peperomia* may be so interpreted. The evidence of these averaged curves is quite different from that of single curves and has the effect of swamping the possible differences of behavior in different individuals. The actual break in the rise of the relative rate may best be sought on the individual curves and is very conclusively shown in the several cases to which attention has already been called. The rarity with which the hourly evaporation rate for Cinchona rises above 16 mg. per hour may be inferred from the small number of readings in table 30 above that amount. The curves (in fig. 12) afford some evidence that the physiological controls which are operative in lowering the relative rate may have operated during the rise of the evaporation from about 5 mg. per hour to 16 mg., while the further rises in relative rate shown for *Pilea* under 23 mg. of evaporation and for *Diplazium* under 20, 23, and 25 mg. doubtless represent the ratios derived from a water loss which is due in large measure to cuticular transpiration, and is beyond the retaining power of any of the normal controls of the plant.

COMPARISON OF RELATIVE TRANSPIRATION RATES IN RAIN-FOREST AND DESERT PLANTS.

Livingston[1] has determined the rates of relative transpiration for several desert annual plants, at the Desert Laboratory at Tucson, Arizona, and Mrs. Edith B. Shreve[2] has secured, at the same place, readings for *Parkinsonia microphylla*, a typical desert perennial, in plants of several ages and seasonal conditions. The possession of these readings, made by the same methods used in my own work, makes possible a comparison of the amounts and limits of relative transpiration in plants of two most widely unlike regions. The species used by Livingston are ephemerals, which complete their life cycle during the summer rainy period, and are typical desert plants in no respect excepting the rapidity with which they grow and come to maturity. His experiments were all made in the sun, but many of his minimum rates of relative transpiration were secured for nocturnal or partly nocturnal intervals. *Parkinsonia microphylla* is a perennial microphyllous tree, which passes a portion of the year in a leafless condition. The experiments of Mrs. Shreve were made on small plants without leaves, and on the twigs of trees, both with and without leaves, as well as on plants grown from seed under hot-house conditions. Her experiments were all performed in the sun with the one exception noted. It will be recalled that all of my own work was carried on in the shade, with the exception of that on *Alchornea*, *Clethra*, and *Dodonæa*.

[1]Livinston, B. E. The Relation of Desert Plants to Soil Moisture and to Evaporation. Carnegie Inst. Wash. Pub. 50, pp. 45–65, 1906.

[2]Shreve, Edith B. The Daily March of Transpiration in a Desert Perennial. Carnegie Inst. Wash. Pub. 194, 1914.

The highest relative rates secured in the Jamaican plants were 0.758 for *Dodonæa* among sun readings, and 0.274 for *Asplenium alatum* among shade readings. Among Mrs. Shreve's readings the highest was a shade reading of 0.818 in a hot-house plant, the highest in an outdoor plant being 0.353 for the branch of a tree in leaf. Livingston's highest readings were 0.785 for *Allionia* and 0.371 for *Boerhaavia*. In short, the highest of the sun readings in Jamaica, taken on one of the most xerophilous shrubs, nearly equals the highest of the sun readings taken by Livingston for *Allionia*, which is one of the many desert ephemerals unable to withstand periods of rainless, sunny weather for more than a fortnight. The maximum readings for *Clethra* and *Boerhaavia* are similar, being 0.351 and 0.371 respectively, and those for *Alchornea* and *Tribulus* happen to be identical: 0.263. A general parallel is thus established between the relative rates in the summer ephemerals of the desert and the most xerophilous of shrubs and trees in the Blue Mountain region. The maximum rates of relative transpiration secured by Mrs. Shreve for *Parkinsonia* range, on the whole, lower, for all of her experiments performed in the sun, than the maxi-

TABLE 30.—*Relation of relative transpiration to increasing evaporation.*

Relative transpiration readings for three species grouped according to the evaporation rate of the interval in which each transpiration reading was secured. The number of readings averaged in each group is indicated.

Evaporation.	Pilea nigrescens.		Peperomia turfosa.		Diplazium celtidifolium.	
	Relative transpiration.	No. of readings.	Relative transpiration.	No. of readings.	Relative transpiration.	No. of readings.
mg.						
0	0.182	1	....	....	....	....
1	.154	4	....	....	....	....
2	.141	3	0.102	3	....	..
3	.123	17	.088	6	0.214	3
4	.078	6	.078	9	.132	3
5	.102	5	.091	8	.109	1
6	.114	9	.098	14	.155	5
7	.085	6	.105	7	.132	4
8	.097	6	.158	2	.146	2
9	.082	1	.046	3	.170	1
10	.090	5	....	..	.197	1
11	.078	4	.079	3	.133	3
12	.051	1	.062	1	.129	1
13	.052	1	.060	4	.139	6
14	....	..	....	..	....	..
15	.078	3	.056	1	.167	4
16	.050	3	.070	6	.088	3
17	....	..	....	..	....	..
18	....	..	....	..	....	..
19	....	..	....	..	....	..
20	....	..	....	..	.172	3
21	....	..	....	..	....	..
22	....	..	....	..	....	..
23	.068	1	.064	1	.133	3
24	....	..	....	..	....	..
25	....	..	....	..	.171	3

mum rates of Livingston for *Tribulus*, *Allionia*, and *Boerhaavia*. Also, my own relative rates for herbaceous species of the rain-forest flora, investigated in the shade, exhibit a lower range of maxima than do the plants used by Livingston. If, however, these rain-forest plants had been placed in the sun their relative rates would have mounted to much higher figures, because of their thin epidermis and light cutinization, taken together with the fact that the high humidity is deterrent to rapid evaporation even in the sun. A test made by placing a plant of *Pilea nigrescens* in full sunshine from $9^h\ 30^m$ to $10^h\ 30^m$ a. m. gave a relative transpiration rate of 0.238, which is twice as great as the highest shade rate secured for this species. The same plant was kept in the sun from $10^h\ 30^m$ to $11^h\ 30^m$ (there being a few minutes of cloudiness in this hour), and the relative rate fell to 0.193, although the evaporation fell only from 22 to 21 mg. Other tests made in the sunshine with the more hygrophilous *Asplenium* and *Diplazium* showed them incapable of withstanding direct insolation for so much as one hour, and although the wilted condition of their leaves indicated a high water loss they were not weighed at the ends of the periods.

The fact that the relative rate of *Pilea* in the shade was doubled by placing the plant in full sunshine gives at least some warrant for estimating that the relative rates of the other herbaceous species would be increased in the sunshine to double their shade values. If such approximate values for the relative transpiration in the sunshine be taken for the herbaceous plants of the rain-forest, they will be of the same general order of magnitude as Livingston's rates for the desert ephemerals, and both of these classes of plants will exceed, in general, the rates secured by Mrs. Shreve for *Parkinsonia*.

The minimum rates of relative transpiration are extremely variable in any number of experiments with the same species, and their significance in comparison is not so great as that of the maximum readings. The highest minimum rates found among the data which are under comparison are those of the hygrophilous ferns of the rain-forest, while the lowest of the rates for *Peperomia basellæfolia* are of the same general order of magnitude as those for the desert ephemerals and for *Parkinsonia* (see table 31).

It is possible to say, in summarizing, that the most nearly xerophilous of the rain-forest plants exhibit about the same maximum relative transpiration rates as do the most nearly hygrophilous of the desert herbaceous species. The relative rates for herbaceous plants of the rain-forest, as determined in the shade, are about half of the rates for the desert ephemerals, as determined in the sun, and there is some evidence that this difference is due to the fact that one set of experiments was performed in the sun and the other set in the shade. The rates for *Parkinsonia*, determined in the sun, are of about the same general order of magnitude as the shade rates for the Jamaican herbaceous species.

In spite of the differences which exist between the maximum relative transpiration rates for the several rain-forest herbaceous plants and for the several species of desert ephemerals, when compared among themselves, a general review of the readings for all of the widely divergent types examined in the work of Livingston, that of Mrs. Shreve, and in my own discovers a much greater uniformity in the amounts of relative transpiration than might be expected in view of the widely dissimilar anatomical characteristics of the plants and the sharply contrasted climates under which they exist.

TABLE 31.—*Showing comparative values of relative transpiration for plants investigated at Tucson, Arizona, and at Cinchona, Jamaica.*

	Maximum.	Minimum.
At Tucson, Livingston's rates:		
Euphorbia, Experiment 1	0.070	0.005
Tribulus, Experiment 4	.263	.008
Tribulus, Experiment 5	.237	.018
Allionia, Experiment 6	.785	.054
Boerhaavia, Experiment 8	.371	.029
At Tucson, Mrs. Shreve's rates:		
Parkinsonia microphylla—		
Leafless seedling, in sun	.213	.084
Do	.136	.034
Leafless branch of tree, in sun	.151	.049
Do	.158	.026
Leafy branch of a tree, in sun	.353	.007
Do	.168	....
Greenhouse plant, in sun	.459	....
Greenhouse plant, in shade	.818	....

	Maximum.	Average.	Minimum.
At Cinchona:			
Clethra occidentalis	0.351	....	0.012
Alchornea latifolia	.263	....	.008
Dodonæa angustifolia	.758	....	.050
Pilea nigrescens, A	.119	0.061	.020
Pilea nigrescens, B	.096	.059	.037
Peperomia stellata, A	.116	.055	.013
Peperomia stellata, B	.112	.058	.026
Peperomia basellæfolia, A	.058	.035	.014
Peperomia basellæfolia, B	.093	.035	.018
Diplazium celtidifolium, A	.169	.099	.056
Diplazium celtidifolium, B	.232	.151	.117
Asplenium alatum, A	.274	.136	.068
Asplenium alatum, B	.251	.138	.078

The total annual evaporation recorded at Cinchona is 32.6 c.c. per square centimeter of free water surface; that at Tucson is 345 c.c. per square centimeter.[1] The two rates are in the ratio of 1 to 10.6. The higher rate of evaporation at Tucson means that in the ratio $\frac{T}{E}$ for that region the values for T must be ten times greater than the

[1]Shreve, F. Rainfall as a Determinant of Soil Moisture. Plant World, 17 : 9–26, 1914.

values for T at Cinchona if a general equality of the ratios exists for the two regions, as has been shown. In other words, the existence of a general equality of maximum relative transpiration between regions of widely diverse climatic conditions, especially with respect to the evaporating power of the air, indicates that there is a rough relation of equality between the maximum transpiring power of the plants native to these regions and the evaporation conditions by which the regions are characterized. In a comparison, then, of the transpiration capacities of plants found in regions with graduated differences of evaporation conditions, it is possible that we may find the transpiration capacities falling into a parallel series of proportional differences.

These statements are not at all in harmony with the commonly accepted view that the transpiration of desert plants is low as compared with that of plants in moist regions. As a matter of fact it is the transpiration of rain-forest plants which is low, and the transpiration of desert plants which is high, in terms of unit areas, and (for Cinchona and Tucson) the rates are roughly proportional to the annual evaporation of the two regions: as 1 is to 10. The question of the

TABLE 32.—*Influence on transpiration exerted by coating upper or lower leaf surfaces.*

Series run in laboratory, with three individuals of *Pilea nigrescens*, by weighing method. First group of readings on uncoated plants, second on plants coated as indicated. Leaf areas (top and bottom): A. 221.8 sq. cm.; B, 326.3 sq. cm.; C, 359.9 sq. cm.

Date.	Hour.	Temperature.	Humidity.	Evaporation.	Uncoated.					
					Pilea A.		Pilea B.		Pilea C.	
					T	$\frac{T}{E}$	T	$\frac{T}{E}$	T	$\frac{T}{E}$
Aug. 5..	9h 00m p.m.	62	90	.....	.....	.....	.....	.....	.....	.....
Aug. 6..	6 00 a.m.	59	90	1.98	0.16	0.081	0.20	0.099	0.45	0.227
	8 00 a.m.	63	85	1.50	.21	.141	.43	.286	.59	.391
	10 00 a.m.	.....	.....	3.06	.83	.272	.88	.286	1.31	.427
	12 00 p.m.	73 ..	83	3.72	.58	.157	.97	.262	1.37	.368
	2 00 p.m.	66	90	6.54	.97	.149	1.73	.264	2.56	.392
	4 00 p.m.	65	93	3.92	.69	.177	.74	.189	1.35	.345
	6 00 p.m.	63	90	3.16	.33	.105	.57	.181	.89	.282
	8 00 p.m.	62	90	3.66	.44	.121	.49	.134	.89	.244

Date.	Hour.	Temperature.	Humidity.	Evaporation.	Lower surface coated.		Uncoated.		Upper surface coated.	
Aug. 6..	9h 45m p.m.	62	90	.....	.....	.....	.....	.....	.....	.....
Aug. 7..	6 00 a.m.	61	95	0.98	.....	.....	.....	.....	0.20	0.201
	8 00 a.m.	62	95	.72	0.08	0.115	0.26	0.365	.39	.538
	10 00 a.m.	66	88	1.44	.30	.208	.60	.417	.61	.426
	12 00 p.m.	.....	.....	3.00	.83	.278	1.24	.415	1.33	.445
	2 00 p.m.	63	95	2.49	.35	.140	.88	.351	1.15	.463
	4 00 p.m.	62	95	2.56	.38	.147	.70	.276	.91	.355
	6 00 p.m.	61	92	2.52	.23	.092	.55	.218	.66	.261
	9 00 p.m.	61	82	4.04	.48	.118	.56	.139	.76	.18

relative amounts of transpiring surface per unit volume in desert and rain-forest plants is, of course, profoundly concerned in the determination of the absolute amounts of water lost by plant individuals. The prevalent conception that plant transpiration is reduced in desert plants arises from a consideration of the reduced transpiring surface of desert plants rather than from a knowledge of their water loss per unit area as compared with hygrophilous plants.

TABLE 33.—*Influence on transpiration exerted by coating upper or lower leaf surfaces.*

Series run in laboratory, with three individuals of *Diplazium celtidifolium*, by weighing method. First group of readings on uncoated plants, second on plants coated as indicated. Leaf areas: (top and bottom): A, 222.6 sq. cm.; B, 227.1 sq. cm.; C, 181.9 sq. cm.

Date.	Hour.	Evaporation.	Uncoated.					
			Diplazium A.		Diplazium B.		Diplazium C.	
			T	$\frac{T}{E}$	T	$\frac{T}{E}$	T	$\frac{T}{E}$
Nov. 18.....	$5^h\ 10^m$ p.m.	.....	.....	.....	.....	.....	.....	.....
Nov. 19.....	9 40 a.m.	8.88	2.23	0.251	2.44	0.275	.....	.....
	11 40 a.m.	13.86	4.23	.305	4.75	.343	.....	.....
	1 40 p.m.	23.55	6.66	.283	7.48	.317	.....	.....
	3 40 p.m.	20.91	6.45	.308	6.87	.328	8.37	0.400
	6 40 p.m.	13.44	3.52	.262	3.27	.244	4.96	.369
Nov. 20.....	9 40 a.m.	5.31	1.58	.298	1.80	.338	2.49	.469
	11 40 a.m.	15.69	5.36	.342	5.61	.358	6.93	.441
	1 45 p.m.	25.05	7.21	.288	8.28	.330	10.22	.408

Date.	Hour.	Evaporation.	Lower surface coated.		Uncoated.		Upper surface coated.	
Nov. 20.....	$2^h\ 15^m$ p.m.	.....	.....	.....	.....	.....	.....	.....
	5 25 p.m.	29.37	3.37	0.114	8.51	0.289	8.37	0.285
Nov. 21.....	8 15 a.m.	12.57	1.36	.109	3.57	.289	3.74	.297
	11 15 a.m.	15.39	1.98	.128	5.91	.386	5.46	.354
	4 15 a.m.	12.18	1.54	.126	4.36	.358	3.95	.324
	7 15 a.m.	10.74	1.24	.116	3.12	.290	3.07	.286
Nov. 22.....	9 45 a.m.	8.64	.92	.106	2.62	.303	2.64	.305

RELATIVE AMOUNTS OF STOMATAL AND CUTICULAR TRANSPIRATION.

The thinness of epidermal wall and lightness of cutinization which are well known to characterize rain-forest plants made it seem desirable to differentiate between stomatal and cuticular transpiration and to attempt an estimation of their comparative amounts. In the lack of a direct method of differentiating between the stomatal water loss and that from the epidermis of both upper and lower leaf surfaces, the following indirect means of obtaining approximate values for them was employed.

Three potted plants of the same species were run simultaneously in order to obtain a calibration of their rates of transpiration with respect to each other. After being run together through one day, the upper

surfaces of the leaves of one plant were coated with molten cocoa butter, the under surfaces of the second were so coated, and the third was left uncoated as a control. In this condition the three plants were again run through one day. It was only after the completion of such a series, the determination of the leaf areas, and the calculation of the results that it was possible to know how evenly matched the rates of the three plants were before coating, and this made necessary such liberal discarding of results that only two such experiments were found to be as satisfactory as might be desired (see tables 22 and 33).

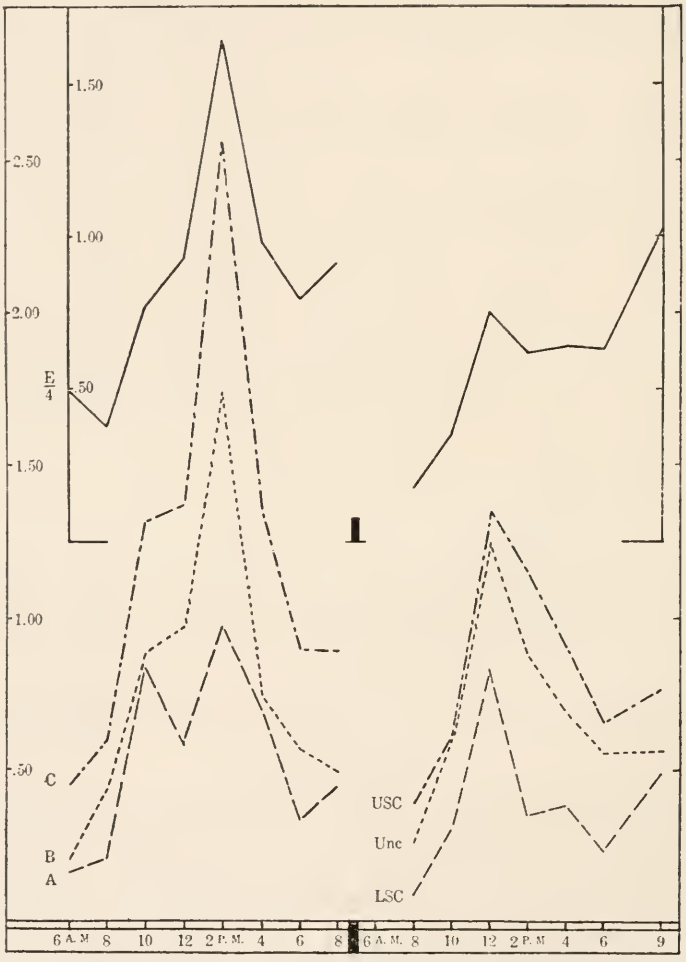


FIG. 13.—Normal daily march of transpiration for three plants of *Pilea*, and march for same plants on succeeding day after leaves of C had been coated on upper surface (USC), those of A had been coated on lower surface (LSC), and those of B had been left uncoated (Unc) as a control. Suspended curve is concurrent evaporation, plotted to one-fourth of scale $\left(\frac{E}{4}\right)$.

It has long been known from the work of Comes[1] that the sum of the transpiration of the lower leaf surface alone and the upper surface alone is greater than the rate from a normal uncoated leaf. I am able to confirm this, as may be seen by comparison of D and E in table 34, indicating an average increase of 34 per cent in top alone plus bottom alone over the uncoated leaf, in *Diplazium* (see fig. 13). I have taken for granted that the amounts by which the transpiration of top alone and bottom alone are increased by coating the opposed surface are proportional to the normal rates themselves, an assumption which can not be far from the truth. On this assumption I have divided the amounts of transpiration in the uncoated plant, hour by hour, into two amounts, which are proportional to the amounts of water loss from the top alone and the bottom alone in the coated plants. This calculation gives the approximate amounts of transpiration for the top and the bottom of an uncoated leaf (G in table 34), hour by hour. As the degree of cutinization is alike on the two sides of the leaves of the plants used, and as the epidermal walls are of almost the same thickness on the two sides, the cuticular transpiration of the bottom of the leaf, the stomata eliminated, is practically the same as that of the top of the leaf. The total area occupied by the stomata is so small as to be practically negligible. The actual stomatal transpiration is, therefore, the difference between the calculated transpiration amounts for the upper and lower leaf surfaces (H, table 34). The values for true stomatal trans-

TABLE 34.—*Showing method used to determine actual stomatal and cuticular transpiration. Diplazium celtidifolium.* (Based on data given in table 33.)

	$5^h\ 25^m$ p.m.	$8^h\ 15^m$ p.m.	$11^h\ 15^m$ p.m.	$4^h\ 15^m$ p.m.	$7^h\ 15^m$ p.m.	$9^h\ 45^m$ p.m.
A. Transpiration of upper surface with lower coated	3.37	1.36	1.98	1.54	1.24	0.92
B. Transpiration of lower surface with upper coated	8.37	3.74	5.46	3.95	3.07	2.64
C. Percentages of A to B (average 37.80 per cent)	40.20	36.40	36.20	38.90	40.60	34.70
D. The sum of A and B	11.74	5.10	7.44	5.49	4.31	3.56
E. Transpiration of uncoated leaves	8.51	3.57	5.91	4.36	3.12	2.62
F. Percentage of increase of D over E (average 34.30 per cent)	38.00	42.70	25.80	25.60	38.20	35.70
G. E divided into amounts proportional to A and B: calculated transpiration upper and lower surfaces in uncoated leaves:						
Upper surfaces	2.44	.95	1.57	1.22	.90	.68
Lower surfaces	6.07	2.62	4.34	3.14	2.22	1.94
H. G-L minus G-U: stomatal transpiration	3.63	1.67	2.77	1.92	1.32	1.26
I. Percentage of H to E (average 45.10 per cent)	42.70	46.70	46.80	44.00	42.30	48.40
J. E minus H: cuticular transpiration	4.88	1.90	3.14	2.44	1.80	1.36
K. Ratio of H to evaporation: relative stomatal transpiration	.123	.132	.179	.157	.123	.147
L. Ratio of J to evaporation: relative cuticular transpiration	.166	.152	.204	.200	.168	.156

[1]Comes, O. Azione della temperatura, della umidita relativa et della luce sulla transpiratione delle piante. Rendic. d. R. Acad. d. Science di Napoli. 1878.

piration (as distinguished from the transpiration of the lower surface) are found to be from 42 to 48 per cent of the total transpiration of the leaf. In other words, in *Diplazium* the total epidermal surface of the leaf loses at all times slightly more water than the stomata.

The relative stomatal and the relative cuticular transpiration have been calculated from these readings (table 34, K, L). A comparison of these two sets of relative transpiration figures shows that the fluctuations in the diurnal march of the relative cuticular rate are only slightly less than the fluctuations of the relative stomatal rate (see fig. 14). This evidence indicates that the irregularities of relative transpiration rate are due to some physiological regulations other than the opening

FIG. 14.—Curves of stomatal transpiration (ST), cuticular transpiration (CT), total transpiration (T), and evaporation $\left(\frac{E}{2}\right)$ for *Diplazium*, together with the rates of relative stomatal transpiration $\left(\frac{ST}{E}\right)$ and relative cuticular transpiration $\left(\frac{CT}{E}\right)$.

and closing of stomata—in other words that the principal regulatory functions reside within the leaf itself and are perhaps active, perhaps passive agents in determining the rate of water loss through the stomata, whatever may be the state of their openness.

The evidence of the curves of relative stomatal and cuticular transpiration depends for its value on the normal stomatal behavior of the plant in which the upper surfaces of the leaves were coated, a matter which could not be investigated during the transpiration weighings, by any available method.

Pilea nigrescens was used in the second experiment, the detailed results of which are not given. In this test the average increase of top alone plus bottom alone over the uncoated leaf was 77 per cent, and the average percentage of the actual stomatal transpiration to the total transpiration of the uncoated leaf was 41 per cent. The latter percentage indicates that the ratio between the stomatal transpiration and the actual total cuticular transpiration is of the same order of magnitude in *Pilea* and in *Diplazium*. The matter of the number of stomata per unit area, which I have not determined, is an important factor in affecting this ratio, as also is the amount of cutinization and thickening of the epidermis.

STOMATAL BEHAVIOR.

The possession of relative transpiration data greatly clarifies the investigation of the influence of fluctuations of stomatal movement on transpiration. The effects of wind, temperature, and humidity are eliminated by their use, and it is possible to compare stomatal condition with the fluctuations of transpiration which are due to internal factors. Such internal factors, whether active or passive in their agency, are alone responsible for the departures of the relative transpiration curve from a straight line parallel to the axis of abscissas.

My purpose in securing readings of stomatal aperture concurrently with transpiration weighings was to learn in how far the changes of stomatal openness might be correlated with the fluctuations of relative transpiration rate. The existence of a positive correlation might be taken as proof of the control of relative transpiration by stomatal movement, or as proof that stomatal movement and the fluctuations of the relative transpiration are both governed by more deep-seated internal factors.

The methods by which I measured transpiration and secured stomatal readings were such that I necessarily obtained my epidermis for the latter purpose from other individuals than those in which the transpiration was being measured. This is an extremely unfortunate limitation to the combined use of the weighing method of determining transpiration and Lloyd's method for stomatal measurement. I secured epidermis from potted plants which had had the same history as those that were being weighed, which looked just like them in general char-

acter of foliage, and were placed alongside them during the intervals between weighings. I am unable to say in how far the results which I am about to give have been modified by the limitations of the methods used. The fact, however, that all of the evidence which I have secured for four species of plants fails to show any serious discordance leads me to believe that the plants used for transpiration and those used for stomata did not behave in such a dissimilar manner as to destroy the validity of my conclusions.

In making measurements of stomatal aperture from the stained and mounted pieces of epidermis, by means of a micrometer eye-piece, I commonly took readings from 24 stomata in each preparation. Unlike other workers who have used this method I did not discard the extreme readings, nor fail to measure the most divergent stomata observed, but measured all stomata throughout a path across the piece of epidermis.

A considerable degree of variability was disclosed in the openness of the stomata in nearly all of the preparations of epidermis. The variability of diameter in two plants, *Peperomia turfosa* and *Diplazium celtidifolium*, is indicated by the data in table 35. *Peperomia* exhibits its widest variability at the first two morning readings, and shows considerable constancy at noon, again becoming variable in the afternoon. *Diplazium* shows a less range of variability, as well as a more constant diameter throughout the day. These are given as typical cases of stomatal variability and they have been treated, as have all other sets of readings, as the normal behavior of the plants concerned,

TABLE 35.—*Variability of stomatal diameter in Peperomia turfosa and Diplazium celtidifolium, October 16, 1909.*

The number of stomata read in diameter groups of 10 microns. Heavy figures indicate the group in which the maximum number of stomata fall.

Hour.	0	0–10	10–20	20–30	30–40	40–50	50–60	60–70	70–80	80–90	90–100	100–110	110–120
PEPEROMIA TURFOSA.													
6 a.m.	...	1	**10**	7	4	1	1	1	2	1	.....	.....	.....
8	4	2	**5**	1	.....	3	4	4	2	1	.....	.....	.....
10	...	.....	2	1	6	6	**7**	5	.....	1	.....	.....	.....
12	...	.....	.....	1	.....	.....	9	**10**	8	.....	.....	.....	.....
2 p.m.	...	.....	.....	.....	.....	1	2	1	8	**8**	3	1	.....
4	...	.....	6	1	3	4	**10**	.....	2	1	.....	.....	.....
6	2	7	**7**	4	5	5	.....	2	.....	.....	.....	.....	.....
9	**14**	9	2	.....	1	1	.....	.....	.....	.....	.....	.....	.....
DIPLAZIUM CELTIDIFOLIUM.													
6 a.m.	...	.....	.....	.....	.....	.....	.....	.....	3	**7**	7	1	.....
8	...	.....	.....	.....	.....	.....	1	1	2	**4**	3	.....	.....
10	...	.....	.....	.....	.....	.....	3	4	3	5	**7**	1	.....
12	...	.....	.....	.....	.....	.....	.....	1	1	**11**	6	3	1
2 p.m.	...	.....	.....	.....	.....	.....	2	6	**7**	6	3	.....	.....
4	...	.....	.....	.....	.....	.....	1	3	**7**	2	6	5	.....
6	...	.....	.....	.....	1	3	**11**	3	4	2	.....	.....	.....
9	...	.....	.....	.....	2	1	**7**	3	4	2	1	.....	.....

and the averages of the variable readings have been used in the tables and curves. As already stated, the measurement of twice the usual number of stomata gave, in no case, a greater difference than 6 per cent between the average diameter of the two groups of 24.

In table 36 and fig. 15 are given the curves for two experiments with *Peperomia turfosa* in which the stomatal readings were taken. The first of these was interrupted at 2 p. m., up to which hour there had been a nearly constant rise of the curves of transpiration and relative transpiration, and a general upward course in the evaporation after 8 a. m. The curve of stomatal openness rises in good agreement with the relative transpiration curve, but reaches a maximum at 12 noon and falls at 2 p. m., in spite of the rise in relative transpiration during the same interval.

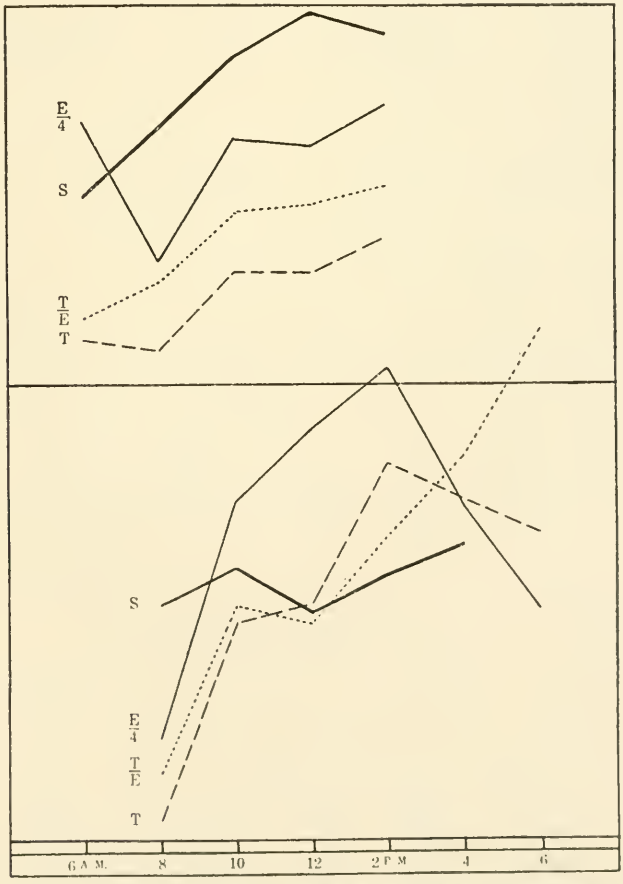


FIG. 15.—Graphs for two experiments with *Peperomia turfosa* in which determination was made of transpiration (T), evaporation $\left(\frac{E}{4}\right)$, relative transpiration $\left(\frac{T}{E}\right)$, and stomatal area (S).

In the second experiment there is a sharp break in the morning rise of the evaporation curve, accompanied by a lessening in the rate of increase of transpiration. These checks are accompanied by a fall in the relative transpiration, which then continues to rise throughout the remainder of the day. The fall in relative transpiration at noon is accepted by a fall in stomatal openness, giving the curves of relative transpiration and stomatal movement a good agreement for the day.

In an experiment with *Pilea nigrescens* (table 37, fig. 16) which was performed along with the first one on *Peperomia turfosa*, already described, and was discontinued at 2 p. m., we have a gradual rise in stomatal openness until 2 p. m., together with a rise in the relative transpiration up to 12 noon, and a slight fall thereafter. The shape of the curves of rise for the two are unlike, and between 12 and 2 p. m. there is the slight fall of relative rate in spite of a continued increase of the stomata. The increase of stomatal openness between 12 and 2 p. m. was greater, in fact, than that between 8 and 10 a. m., but in the latter case there was a sharp rise in the relative rate, accompanying a rapid rise of evaporation. The 6 a. m. readings of evaporation and transpiration in this

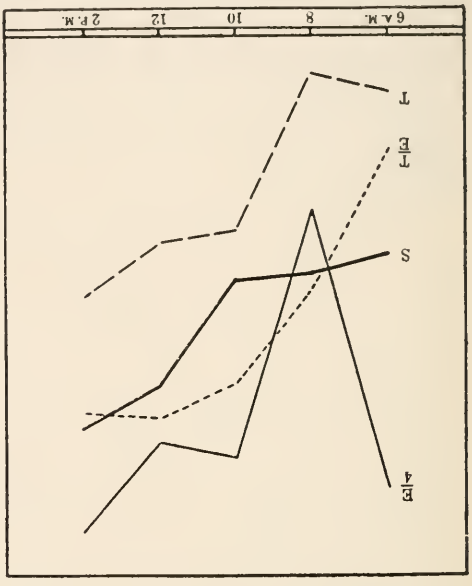


FIG. 16.—Graphs for evaporation $\left(\frac{E}{4}\right)$, and for transpiration (T), relative transpiration $\left(\frac{T}{E}\right)$, and stomatal area (S) of *Pilea nigrescens*.

TABLE 36.—*Transpiration, relative transpiration, and stomatal behavior in Peperomia turfosa.*

Series run in laboratory; transpiration by weighing method; stomata from potted plants under same conditions as those weighed.

Date.	Hour.	Evaporation.	T	$\frac{T}{E}$	Stomatal width.	Stomatal length.	$\sqrt{w \times l}$
July 30.....	6 p.m.	....	....	....	....	....	....
July 31.....	6 a.m.	6.96	0.31	0.044	2.4μ	16.1μ	6.22
	8	3.24	.23	.069	3.6	19.9	8.47
	10	6.48	.74	.114	5.1	22.9	10.80
	12 p.m.	6.30	.74	.118	6.2	24.2	12.25
	2	7.44	.97	.131	5.4	24.9	11.55
Aug. 17....	9 p.m.	.....	....	....	...	....	.....
Aug. 18....	8 a.m.	2.64	.12	.044	3.5	17.2	7.76
	10	9.00	1.44	.155	4.5	18.2	9.04
	12 p.m.	10.92	1.56	.143	4.1	13.8	7.52
	2	12.42	2.50	.202	4.6	16.9	8.82
	4	8.94	2.26	.254	5.4	17.7	9.78
	6	6.18	2.03	.337	...	....	.....

experiment are from over-night readings, and are not to be correlated with the stomatal conditions at 6 a. m.

On October 16 simultaneous determinations of stomatal openness were made on *Peperomia turfosa, Pilea nigrescens, Diplazium celtidifolium,* and *Asplenium alatum,* in connection with transpiration and evaporation readings (table 38, figs. 17 and 18). *Peperomia turfosa*

TABLE 37.—*Transpiration, relative transpiration, and stomatal behavior in Pilea nigrescens.*

Series run in laboratory; transpiration by weighing method; stomata from accompanying potted plants.

Date.	Hour.	Evaporation.	T	$\frac{T}{E}$	Stomatal width.	Stomatal length.	$\sqrt{w \times l}$
July 30.....	6 p.m.	....	....	....	...	....	....
July 31.....	6 a.m.	6.96	0.43	0.062	2.2	10.3	4.76
	8	3.24	.38	.116	2.5	10.2	5.10
	10	6.48	.89	.138	2.5	10.8	5.20
	12 p.m.	6.30	.93	.149	3.8	12.9	7.00
	2	7.44	1.10	.148	4.5	12.9	7.62

TABLE 38.—*Transpiration, relative transpiration, and stomatal behavior in five species investigated simultaneously.*

Series run in laboratory; transpiration by weighing method; stomata from accompanying potted plants.

Date.	Hour.	Evaporation.	Peperomia turfosa.					Pilea nigrescens.				
			T	$\frac{T}{E}$	Stomatal width.	Stomatal length.	$\sqrt{w \times l}$	T	$\frac{T}{E}$	Stomatal width.	Stomatal length.	$\sqrt{w \times l}$
Oct. 16	6 a.m.	6.36	0.21	0.033	3.1	21.0	8.08	0.23	0.036	3.2	11.6	6.09
	8	4.50	.13	.028	3.8	17.2	8.09	.19	.041	3.1	11.3	5.92
	10	11.77	.77	.066	4.8	20.5	9.92	.79	.067	3.4	12.6	6.53
	12 p.m.	23.01	1.48	.064	6.5	23.0	12.23	1.58	.068	4.5	16.7	8.67
	2	16.20	.78	.049	7.9	19.8	12.51	1.05	.064	5.6	14.5	9.01
	4	13.95	.39	.028	4.4	19.4	9.24	.73	.052	.8	16.0	3.62
	6	16.72	.37	.022	2.5	17.9	6.68	.33	.020	2.3	11.8	3.58
	9	7.80	.10	.013	.6	20.7	3.52	.19	.024	2.2	12.6	5.26

Date.	Hour.	Evaporation.	Diplazium celtidifolium.					Asplenium alatum.				
			T	$\frac{T}{E}$	Stomatal width.	Stomatal length.	$\sqrt{w \times l}$	T	$\frac{T}{E}$	Stomatal width.	Stomatal length.	$\sqrt{w \times l}$
Oct. 16	6 a.m.	6.36	0.70	0.111	8.3	22.1	13.54	1.02	0.160	4.5	15.7	8.40
	8	4.50	.42	.094	8.2	19.5	12.64	.66	.147	4.9	16.0	8.86
	10	11.77	1.17	.099	8.1	18.4	12.21	1.43	.122	5.2	15.0	8.83
	12 p.m.	23.01	2.32	.100	8.9	20.2	13.37	2.41	.105	.....	.....	.....
	2	16.20	1.60	.098	7.6	18.5	11.85	1.92	.118	5.0	14.2	8.43
	4	13.95	1.01	.072	8.0	20.6	12.85	1.30	.093	4.7	19.9	9.68
	6	16.72	.93	.055	6.0	21.0	11.22	1.14	.068	2.4	12.8	5.54
	9	7.80	.64	.082	6.4	21.2	11.65	1.36	.111	3.9	16.9	8.12

shows a maximum of the daily relative transpiration at 10 a. m., the maximum for evaporation and transpiration at 12 noon, and the maximum of stomatal aperture at 2 p. m. Between 10 and 12 a. m. there was a pronounced increase in the stomatal openness, which was accom-

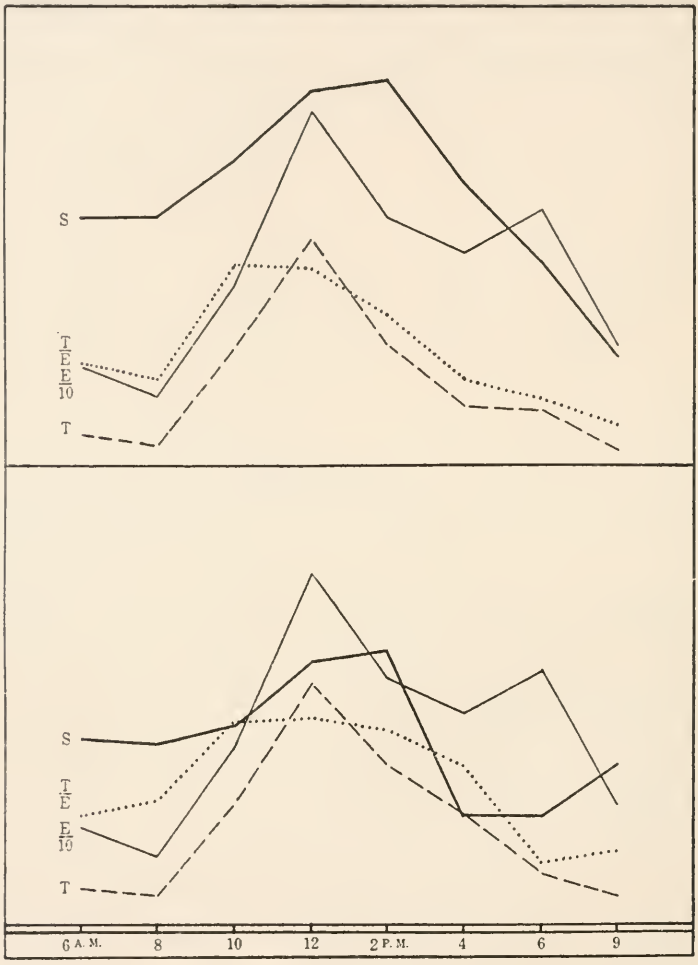


FIG. 17.—Curves for simultaneous experiments with *Peperomia turfosa* (upper) and *Pilea nigrescens* (lower) which determination was made of transpiration (T), relative transpiration $\left(\frac{T}{E}\right)$, stomatal area (S), and evaporation $\left(\frac{E}{10}\right)$.

panied by a plateau in the curve of relative transpiration. Between 12 and 2 p. m. there was a considerable fall in the relative rate at the same time that the stomatal aperture was still increasing. The curves for *Pilea* show a general similarity to those for *Peperomia*: there is the

daily maximum of transpiration and evaporation at 12 noon, with a plateau in the curve of relative transpiration between 10 a. m. and 2 p. m., accompanied by a sharp rise in the curve of stomatal openness between 10 a. m. and 12 noon, and a less rise between 12 and 2 p. m.

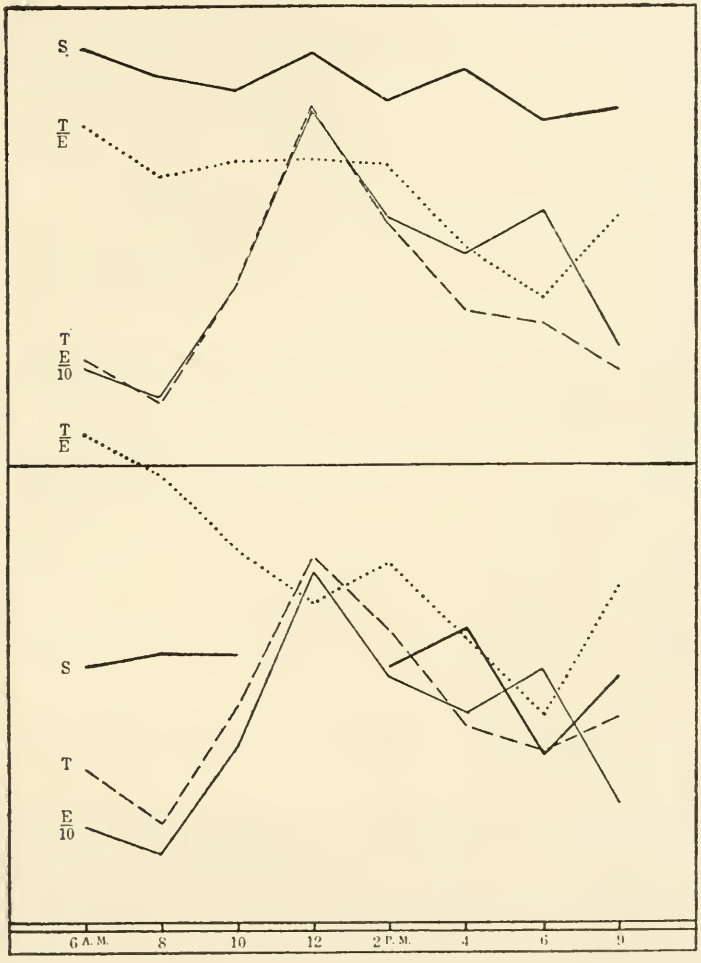


FIG. 18.—Curves for simultaneous experiments with *Diplazium celtidifolium* (upper) and *Asplenium alatum* (lower). These experiments were carried out on the same day as those with *Peperomia* and *Pilea* (fig. 17). The curves are: transpiration (T), evaporation $\left(\frac{E}{10}\right)$, relative transpiration $\left(\frac{T}{E}\right)$, and stomatal area (S).

In the afternoon, between 4 and 6 o'clock, there is a rapid fall in the relative rate, with no accompanying change in the stomatal openness; between 6 and 9 p. m., however, the two rise in company.

The daily march of stomatal openness for *Diplazium* is extremely uniform. The transpiration of the plant followed the evaporation

with remarkable exactness from 6 a. m. until 2 p. m., after which hour it continued to fall during the occurrence of a secondary maximum of evaporation, culminating at 6 p. m. There is as much disagreement as there is agreement in the curves of relative transpiration and stomata movement from 6 a. m. to 4 p. m. The close parallelism of the transpiration and evaporation curves is very striking as compared with the divergent behavior of the relative transpiration and stomatal curves and points to the impotence of stomatal movements in counteracting the influence of evaporation rate on transpiration, at least during the mid-day hours. From 4 p. m. until 9 p. m. the curve of transpiration lay below that of evaporation (plotted as one-tenth of the actual readings), and during these hours there is a certain degree of correlation between the relative transpiration and stomatal behavior: they fall together from 4 to 6 p. m., but the rise in the relative rate between 6 and 9 p. m. is too great to be accounted for by the slight rise in stomata openness.

The series of stomatal readings for *Asplenium* is unfortunately marred by the loss of the 12 noon datum. Even in its absence, however, it is possible to observe the fall of relative rate between 8 and 10 a. m., accompanied by a constant stomatal openness, and the pronounced fall of relative rate between 2 and 4 p. m., during an increase in stomatal aperture. Here again, as in the case of *Diplazium*, there is a close parallel between the rates of transpiration and evaporation until 4 p. m. after which hour there is a parallelism between relative transpiration and stomatal behavior that is entirely lacking through the earlier part of the day. The opening up of the stomata between 6 and 9 p. m. in *Diplazium* is still more pronounced in *Asplenium*, where the transpiration rises with it. This occurs in both plants in spite of a sharply falling rate of evaporation, and this also occurred at the same time in *Pilea nigrescens* (fig. 17).

If a correlation of relative transpiration and stomatal movement is to be interpreted as proving that the latter controls the former, the total evidence which I have secured indicates that stomatal movements are of minor importance in regulation of transpiration. The lack of a constant correlation between the relative transpiration behavior and stomatal movement bears also on the question of the regulation of stomatal openness by the water-content and other conditions of the leaf, a problem on which I have no data.

My experiments show, in general, that there is a lack of correlation between the relative transpiration and stomatal movements during the mid-day, and that in the late afternoon and early night there is a positive correlation. This means that the evaporating power of the air and the water-losing capacity of the plant stand in such a close correlation during mid-day that the degree of stomatal aperture is incapable of exerting a positive controlling influence. Under the lower

evaporation of the late afternoon and early night, and in the absence of light—which is always to be reckoned with in its immediate effects on transpiration—the conditions of stomatal openness are capable of an apparent regulation of relative transpiration.

TABLE 39.—*Influence of darkness on transpiration.*

Amounts of transpiration and relative transpiration for *Pilea nigrescens* and *Peperomia turfosa* in the diffuse light of the laboratory and in a dark chamber. Humidity was determined by psychrometer and by polymeter.

Date.	Hour.	Temperature.	Humidity.		Evaporation.	Pilea nigrescens, A.		Pilea nigrescens, B.		Peperomia turfosa.	
			Psy.	Pol.		T	$\frac{T}{E}$	T	$\frac{T}{E}$	T	$\frac{T}{E}$
Sept. 17.	6h 00m p.m.	66	95	98	.....	.....	.....	.....	.....	.....	.....
Sept. 18.	9 30 a.m.	69	91	94	1.26	0.10	0.080	0.16	0.124	0.08	0.067
	11 30 a.m.	75	87	86	10.12	1.08	.107	1.35	.133	.88	.087
	1 30 p.m.	69	91	93	15.30	1.08	.070	1.49	.097	.62	.040
	3 30 p.m.	69	89	90	8.77	.67	.071	.86	.098	.31	.036
	6 30 p.m.	67	93	97	10.10	.64	.063	.88	.087	.38	.037
Sept. 19.	9 30 a.m.	67	.....	97	3.90	.23	.061	.30	.078	.07	.017
	7 30 p.m.	66	.....	96	3.38	.28	.085	.37	.110	.13	.038
Sept. 20.	8 40 a.m.	60	.....	98	3.62	.19	.052	.26	.074	.09	.024
	6 30 p.m.	66	.....	97	2.44	.20	.083	.31	.130	.07	.030
Averages in light:											
1 nocturnal reading							0.080	.....	0.124	.....	0.067
4 diurnal readings							.078	.....	.104	.....	.050
Averages in darkness:											
2 nocturnal readings							.056	.....	.076	.....	.021
2 diurnal readings							.084	.....	.120	.....	.034

INFLUENCE OF DARKNESS ON TRANSPIRATION.

The securing of relative transpiration rates is of great value in the investigation of the influence of individual factors on the rate of transpiration. It is impossible, for example, to determine the rate of transpiration of a plant in the light and then to place it in darkness without changing other factors than the light. Such changes, notably in air movement and humidity, are of strong influence upon the rate of absolute transpiration, but without influence on the relative rate. I was interested in the influence of darkness on transpiration in connection with the general question of stomatal behavior and in connection with the relation between the diurnal and nocturnal transpiration activities of rain-forest plants. With the means at hand to secure relative transpiration rates, I made two tests of the rate for plants placed first in the diffuse light of the physiological laboratory, and afterwards in the dark chamber which has been described.

The first test (table 39) involved two plants of *Pilea nigrescens* and one of *Peperomia turfosa*. The series was run over night and through one day in the light, and was then placed in darkness for 48 hours, readings being taken each morning and evening. On comparing the rates of relative transpiration for the first night and the averaged rates for the day in the light, the latter will be found to be the lower of the two. The rates for the first night were, however, considerably higher than those for the two nights in the dark chamber. The averaged rates for the day in the light are lower than the diurnal readings in the dark chamber in the case of *Pilea*, but are higher in *Peperomia*. The rates for the first and second days and for the first and second nights in the dark chamber are in fairly close agreement. The evidence of the two plants of *Pilea* is in agreement in showing an increase in relative rate due to darkness, while *Peperomia* shows a decrease in rate.

TABLE 40.—*Influence of darkness on transpiration.*

Amounts of transpiration and relative transpiration for five species, in the diffuse light of the laboratory and in a dark chamber.

Date.	Hour.	Temperature.	Humidity.	Evaporation.	Pilea nigrescens.		Peperomia turfosa.		Peperomia basellæfolia.		Diplazium celtidifolium.		Asplenium alatum.	
					T	$\frac{T}{E}$	T	$\frac{T}{E}$	T	$\frac{T}{E}$	T	$\frac{T}{E}$	T	$\frac{T}{E}$
Oct. 11	7h 00m a.m.	63	92	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....
	9 00 a.m.	70	89	3.07	0.34	0.111	0.21	0.068	0.18	0.058	0.52	0.169	0.84	0.274
	11 00 a.m.	73	83	12.00	.75	.051	.76	.063	.57	.048	1.12	.093	1.55	.129
	1 00 p.m.	72	83	16.12	1.09	.067	.92	.057	.66	.041	1.43	.089	1.80	.112
	3 00 p.m.	69	89	15.52	1.03	.066	.87	.056	.48	.031	1.25	.080	1.56	.100
	5 00 p.m.	67	90	11.02	.57	.051	.50	.046	.25	.023	.87	.079	1.23	.112
	7 00 p.m.	64	93	5.85	.26	.044	.15	.026	.20	.035	.44	.076	.64	.109
	9 00 p.m.	63	92	4.27	.19	.045	.31	.074	.17	.039	.41	.097	.63	.147
Oct. 14	3 30 p.m.	.....	74	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....
Oct. 15	9 30 a.m.	.....	85	7.61	.31	.041	.20	.027	.23	.030	1.23	.096	1.06	.139
	3 30 p.m.	.....	85	6.07	.55	.090	.29	.048	.34	.056	1.20	.115	1.12	.185
Average of 7 readings in light						0.062		0.056		0.039		0.098		0.140
Average of 2 readings in darkness						.065		.038		.043		.106		.162

The second experimental series (table 40) involved the five species which have heretofore been mentioned: *Pilea nigrescens*, *Peperomia turfosa*, *Peperomia basellæfolia*, *Diplazium celtidifolium*, and *Asplenium alatum*. These plants were run in diffuse light on October 11, and three days later were run in the dark chamber from mid-afternoon until mid-morning of the following day, and again to mid-afternoon of the second day. The time of taking these readings is such that nocturnal and diurnal rates in the darkness can not be compared. A comparison of the averaged rates for the seven readings in the light with the single diurnal rate in the darkness shows that the darkness rate was higher

for all of the species excepting *Peperomia turfosa*. A comparison of the averaged rates in the light with the average of the two sets of darkness readings, nocturnal and diurnal, brings out the same behavior, in which *Peperomia turfosa* is the only form showing a lowering of rate due to darkness.

In each of the experiments and in each plant investigated there was a maximum of relative transpiration in the light which was well in excess of the darkness rate. Rates which approach the daily maximum in amount are, however, of infrequent occurrence in series of two-hour readings, with the result that daily averages are low as compared with the maximum rates.

The influence of darkness on the aperture of stomata was briefly investigated in *Pilea nigrescens* and *Peperomia turfosa*. Plants of these species were placed in a dark chamber for three days, and at the end of the period material for stomatal examination was taken in the usual manner, without exposing the plants to any more light than was necessary for the operation. The resulting measurements give for *Pilea*: width 5.24μ, length 14.01μ; *Peperomia*: width 5.39μ, length 20.17μ. The values for $\sqrt{l \times w}$ are respectively: 8.53 and 10.43. For plants in the light, the figures given for stomatal aperture in *Pilea* (table 37 and 38) show daily maxima of 7.62 and 9.01, readings with the average of which the darkness aperture of 8.53 is in near agreement. The daily maxima in the light, as determined for *Peperomia* (tables 36 and 38) are 12.25, 9.78, and 9.01, amounts which are also of the same order of magnitude as the darkness determination of 10.43.

Lloyd states[1] that in plants of *Verbena ciliata* placed in prolonged darkness the stomata perform the usual nocturnal closure and remain closed. Several earlier workers, using various and usually unreliable methods, have stated that there is an opening of stomata in prolonged darkness, usually following a closure during the first few hours.

While I can not maintain from single readings on two plants that the stomata are constantly as wide open in darkness as the above figures indicate, nevertheless the probability is extremely strong that none of the possible fluctuations of aperture in darkness carry the stomata to a degree of openness much below the possible normal daily maximum under light conditions. It will be seen from the data in table 28 that *Pilea* and *Asplenium* show a sharp increase of stomatal area between 6 and 9 p. m., while *Diplazium* shows a slight increase—behavior which is in accordance with the readings taken in darkness and is indicative of a possible failure of the stomata to close on first being placed in darkness. No other results were secured which throw light on this matter.

The fact that the stomata of plants placed in prolonged darkness show a degree of openness similar to the somewhat transitory daily

[1]Lloyd, F. E. The Physiology of Stomata, p. 115. Carnegie Inst. Wash. Pub. 82, 1908.

maximum of plants in light, and that such a degree of openness is probably maintained throughout the 24 hours, is in accordance with the high rates of relative transpiration already stated as occurring in plants placed in darkness. Livingston has reported[1] a higher rate of relative transpiration by night than by day for certain species of cacti, a phenomenon in which stomatal behavior is probably not concerned. Although stomatal behavior has been shown in a preceding section not to be the controlling factor in the diurnal fluctuations of transpiration in the rain-forest plants which I have investigated, it does show an increasing tendency toward such control in the later hours of the day, and the results just given indicate that the wide openness of stomata in prolonged darkness is responsible for the high rates of relative transpiration in darkness, I have no evidence calculated to explain the aberrant behavior of *Peperomia turfosa*, in which the relative rate is lowered in the darkness.

INFLUENCE OF HIGH HUMIDITY ON TRANSPIRATION.

The retarding influence of high percentages of humidity on the rate of absolute transpiration is well known both upon experimental and theoretical grounds. I have taken the opportunity to investigate the rates of absolute and relative transpiration under conditions of high humidity in the five species already mentioned as used in other experimental work. The plants were placed in the moist chamber which has been described, and the humidity was kept above 90 per cent and usually above 95 per cent, the percentage being determined by means of a Lambrecht polymeter, calibrated for high humidities by use of a sling psychrometer. The results as respects absolute transpiration are what was expected—there is a decided cutting down of the rate. The

TABLE 41.—*Transpiration of Pilea and Peperomia at high humidities.*

Series run in moist chamber in diffuse light of laboratory.

Date.	Hour.	Temperature.	Humidity.	Evaporation.	Peperomia turfosa.		Pilea nigrescens.	
					T	$\frac{T}{E}$	T	$\frac{T}{E}$
Sept. 8.....	2 p.m....	75	95	.....	.....	.....	.....	.....
	10 p.m....	62	98	3.30	0.16	0.048	0.31	0.095
Sept. 9.....	6 a.m....	59	98	1.33	.04	.031	.12	.093
	2 p.m....	73	95	.67	.09	.144	.25	.380
	10 p.m....	59	98	2.98	.11	.038	.37	.125
Nocturnal reading.....						0.031	.....	0.093
Average of 3 diurnal readings.....						.077	.....	.200

[1]Livingston, B. E. Relative Transpiration in Cacti. Plant World, 10: 110–114, 1907.

rates of relative transpiration, however, are not sharply reduced; in fact they are either of the same order of magnitude as in other experiments already commented on, or are even greater than in them (compare tables 41, 42, and 43, showing rates at high humidities, with tables 23, 24, and 25). This is equivalent to saying that the degree to which the conditions of high humidity cut down water loss from the plant is equalled or exceeded by the rate at which they reduce the water loss of the atmometer. I have already called attention to the correcting

TABLE 42.—*Transpiration of Pilea and Peperomia at high humidities.*

Series run in moist chamber.

Date.	Hour.	Temperature.	Humidity.	Evaporation.	Pilea nigrescens, A.		Pilea nigrescens, B.		Peperomia turfosa.	
					T	$\frac{T}{E}$	T	$\frac{T}{E}$	T	$\frac{T}{E}$
Sept. 20	6h 30m p.m.	66	97	.....	.....	.....	.....	.....	.....	.....
Sept. 21	9 00 a.m.	66	98	0.73	0.03	0.039	0.02	0.027	0.01	0.011
	6 00 p.m.	65	98	1.58	.17	.109	.30	.195	.20	.129
Sept. 22	9 00 a.m.	65	98	1.07	.06	.053	.06	.057	.12	.114
	5 00 p.m.	64	98	1.18	.26	.110	.31	.131	.16	.067
Sept. 23	10 00 a.m.	67	98	.21	.01	.025	.06	.145	.01	.028
	5 45 p.m.	65	98	1.15	.26	.115	.52	.227	.25	.109
Average of 3 noeturnal readings						.039	.....	.076	.....	.051
Average of 3 diurnal readings						.111	.....	.184	.....	.102

TABLE 43.—*Transpiration of five species at high humidities.*

Series run in moist chamber.

Date.	Hour.	Average temperature.	Average humidity.	Evaporation.	Pilea nigrescens.		Peperomia turfosa.		Peperomia basellæfolia.		Diplazium celtidifolium.		Asplenium alatum.	
					T	$\frac{T}{E}$	T	$\frac{T}{E}$	T	$\frac{T}{E}$	T	$\frac{T}{E}$	T	$\frac{T}{E}$
Oct.	9h 30m a.m.	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....
14	11 30 a.m.	72.9°	93.9+	.60(?)	0.46	.....	0.36	.....	0.20	.....	0.51	.....	0.74	.....
	1 30 p.m.	79.8	98.0	2.55	.58	0.228	.70	0.277	.37	0.146	.720	0.285	1.01	0.396
	3 30 p.m.	75.4	92.4	6.30	.61	.097	.35	.056	.29	.046	.59	.093	.70	.110

factor which must be introduced in comparing atmometric readings taken in climates of distinctly unlike conditions of atmospheric humidity. The differences in the character of the water films presented by the atmometer under arid and under humid conditions would not be manifested between atmospheric conditions as similar as those in my moist chamber and those normally prevailing in the physiological laboratory at Cinchona, or would, at least, be so small as to be negligible.

The rates of absolute transpiration obtained under moist-chamber conditions are of importance in the general correlation of my experimental work at Cinchona with my instrumentation within the rain-forest proper. I have already alluded to the difference between the humidity and cloud conditions on the windward and leeward slopes of the Blue Mountains. My moist chamber experiments were performed under conditions more nearly like those of the Windward Ravines and Windward Slopes; the other laboratory experiments, however, were carried on under the normal shade conditions of the Leeward Slopes, on which the laboratory is situated. The low rates of absolute transpiration secured in the moist chamber may be taken as closely paralleling the rates in the still air of Windward Ravines and in Windward Slopes throughout the greater part of all normal days. In spite of the approximate equality of the relative transpiration rates secured in the moist chamber and those secured in the open laboratory, the fact remains that the evaporation rate of the moist chamber and of the moist habitats of the rain-forest is extremely low, and the equality of the relative rates merely indicates that the transpiration is correspondingly low in the latter situations.

TABLE 44.—*Coefficients of transpiration for open laboratory and for moist chamber.*

	Laboratory.	Moist chamber.
Pilea nigrescens (Windward Slope)	1.64	1.79
Peperomia turfosa (Windward Slope)	1.54	1.58
Peperomia basellæfolia (Ridge)	1.00	1.00
Diplazium celtidifolium (Windward Ravine)	3.38	1.98
Asplenium alatum (Windward Ravine)	3.57	2.58

The plants of the Windward Ravines which were brought for experimentation into the somewhat drier atmospheric conditions of the laboratory at Cinchona were subjected thereby to more active water loss. The plants of the Windward Slopes and Ridges which were brought into the laboratory were not subjected to so great a change from the conditions prevailing in their natural habitats. By reason of this circumstance it is instructive to compare the rates of transpiration of the several species *inter se* under each of the two sets of experimental conditions: the moist chamber and the open laboratory. It is possible by such a comparison to determine whether the rates of transpiration of the several species from different habitats stand in the same relation to each other under the Leeward Slope conditions of the laboratory at Cinchona and the Windward Ravine conditions of the moist chamber. This is best done by totaling the amounts of absolute transpiration for simultaneous periods and reducing the totals to the basis of the lowest as unity. Such figures have already been given for the labora-

tory series with five species, and the figures are here repeated (table 44) for comparison with the rates for the moist chamber series (table 43).

A comparison of the two columns of figures shows the first three plants to stand in approximately the same relation to each other under the two sets of conditions. The two ferns from the Windward Ravines, however, exhibit lower rates of transpiration in comparison with *Peperomia basellæfolia*, as well as the other species, under moist-chamber conditions. The significance of this fact is that the average play of atmospheric conditions in the laboratory at Cinchona was less humid than it is in the natural habitat of the two ferns, and they were consequently exposed to a water loss greater than that which would take place in the Windward Ravines. In other words, the two ferns were subjected to a greater acceleration of transpiration by removal from the rain-forest than were the other three species of the less humid habitats. Such behavior on the part of *Diplazium* and *Asplenium* is abundantly explained by the lightness of their epidermal water-conserving structures. In none of the experiments with these species were they observed to wilt or show the least sign of loss of general turgidity, although such appearances could be readily secured by exposing them to half an hour of sunshine. The transpirational behavior of the ferns in the shade of the laboratory is, therefore, normal in its character, although the water losses are themselves higher in amount than in the Windward Ravines (see p. 67 and p. 76).

GENERAL CONCLUSIONS.

Jamaica presents typical insular tropical conditions, with a rainy windward coast, a leeward dry coast, and an intervening cool mountain region. The interesting changes of vegetation between sea-level and 4,500 feet (1,370 meters) have been so seriously modified by human interference as to be only imperfectly recognizable. Above this elevation, however, is an almost unbroken cover of virgin vegetation, in which the floristic and vegetational changes are relatively slight from 4,500 feet to the highest summit, at 7,428 feet (2,265 meters). This undisturbed montane region is characterized by a rainfall of from 105 inches (268 cm.) to 168 inches (427 cm.), and by the prevalence of a cloud blanket which is particularly persistent over the windward slopes of the mountains. The prevailing vegetation is a type of rain-forest which possesses an intermingling of tropical and temperate characteristics, and a floristic admixture of genera from the adjacent lowlands and from the north temperate zone.

Within the rain-forest region the major distinction of climate and vegetation is that which exists between the windward and leeward slopes of the main mountain mass, which lies nearly at right angles to the direction of the trade winds. On both sides of the mountains minor distinctions may be made between the vegetation of ravines, slopes, and ridges. The effects of rain, fog, and wind are modified by the erosion topography in such a manner as to make the Ravines the most hygrophilous habitats, the Ridges the least hygrophilous, and the Slopes intermediate between the two. The forests of the ridges are essentially alike on both windward and leeward slopes, but those of the Windward Ravines and Leeward Ravines, as well as those of the Windward Slopes and Leeward Slopes, present substantial differences. The most important physical factor concerned in the differentiation of these habitats is atmospheric humidity, although this is, in turn, conditioned by the prevalence of fog.

The Windward Ravines exhibit most strikingly the characteristics of the rain-forest, some of which are lacking in each of the other habitats. No one of the forest types occupying the five habitats may be looked upon as possessing a closer adjustment to its own complex of physical conditions than does any of the others. No one of the types can emerge from its own habitat, and under no possible physiographic change of the region can any one of these habitats come to occupy all, or even a preponderant part, of the region. In other words, there is no means by which it might be possible to fix upon any one of the five types as representing the so-called "climax" forest of the Jamaican montane region.

The topography is of prime importance for the distribution of the vegetation, for it is the agency by which the physical conditions are given their local modifications, and these modifications are in turn responsible for the distribution of the forest types. Changes in the topography are active, through erosion, but their operation leaves the relief of the mountains essentially unaltered as they are gradually worn down. There is no respect in which the progress of physiographic change alters the adjustment of physical conditions or the distribution of the habitats, excepting perhaps the case in which a ravine may broaden and eventually become a part of the larger slope down which the ravine formerly drained. Although the eroding power of a heavy tropical rainfall is rapidly carrying the montane region toward base-level, the only discoverable outcome of the process is that the present vegetation, with all of its present habitat distinctions, will gradually be carried down to a level at which climatic changes will dominate the history of the vegetation. The existence of two small areas of alpine meadow on high peaks at the present time would indicate that such has been the fate of types of vegetation that formerly occupied the higher elevations.

Any successional phenomena which might be discoverable in the montane rain-forests, whether due to such physiographic change as the merging of a maturing ravine into its mother slope or to such climatic change as would cause a relict alpine meadow to be invaded by forest, would in any case resolve themselves into a matter of the gradual change of vegetation in dependence upon a gradual change of physical environment. The relation of the old vegetation to its environmental conditions, and the relation of the succeeding vegetation to its environmental complex are both matters that would far outweigh in importance the floristic and ecological features of the succession itself.

Under the conditions of equable temperature and abundant water supply which obtain in the rain-forest, there are no climatic checks to the continual activity of the plants. The annual periodicities of growth and flowering are, however, greatly diversified, there being unbroken activity in some species and a well-marked winter season of rest in others. It may be said, in general, that the former species are those of tropical lowland relationship and the latter are those belonging to north temperate genera. It is to the inherited differences of physiological constitution between these groups of plants that we must look, by experimental means, to an understanding of their divergence of behavior under identical physical conditions.

The rate of growth in the montane rain-forest region is much slower than it is in the vegetation of the lowlands. The uncoiling leaves of tree-ferns and the leaves of some of the large herbaceous ferns exhibit a rapid rate of elongation. The growth of leaves is moderately rapid in the shrubs and trees which are in continuous or nearly continuous

activity, but is slow in the majority of common trees, including those which are completely defoliated in the winter months. Extremely slow rates of growth prevail among the trees which possess the most sclerophyllous types of foliage, and also among the herbaceous flowering plants of the forest floor.

The normal daily course of weather conditions in the rain-forest region is such that the total daily water loss of all plants is extremely low. The trees and shrubs are capable of relatively high rates of transpiration in full sunshine, but there are few days in which these rates are maintained for more than three or four hours in the early morning and perhaps an additional hour or two in the afternoon. The hygrophilous plants of the floor of the Windward Ravine forest are incapable of withstanding insolation for more than one or two hours, even at high humidities, without wilting. When brought into the climate of the Windward Slopes these plants lose from 3 to $3\frac{1}{2}$ times as much water per unit area as do the herbaceous plants of the least hygrophilous habitat, the Ridge Forest. When placed in the moist atmosphere of their own habitat the Windward Ravine plants lose only 2 to $2\frac{1}{2}$ times as much water as the plants of the Ridge Forest. The open mesophyll and thin epidermis of the hygrophilous ferns enables them to maintain surprisingly high rates of transpiration in the shade, in an atmosphere of very high humidity; the rates of water loss per unit area are only half as great in the herbaceous flowering plants of the Ravines and Slopes, and from one-third to one-fourth as great in the plants of Ridges and in the epiphytic orchids.

The prevailing conditions of the interior of the rain-forest are inhibitory to transpiration and also to photosynthesis. The constant high humidities and the dull light which prevails may well be responsible, through these functions, for the prevailing low rates of growth. The lowness of the temperature within the forest, and possibly also its equable character, are also connected intimately with the slow operation of the individual functions of the plant and with the cumulative effect upon growth.

When the transpiration rates of rain-forest plants are converted into rates of relative transpiration, and thereby correlated with the prevailing atmospheric conditions which are the determinants of the rate of evaporation and are the chief external factors determining transpiration rate, they are then found not to be low. The rates of relative transpiration in Jamaican rain-forest plants and in plants of the Arizona desert are found to be of the same general order of magnitude. This is merely saying that the rates of transpiration in the two regions are proportional to the rates of evaporation which prevail in them. While the plants of the rain-forest are capable of losing much more water per unit area than are the plants of the desert if the two kinds of plants are brought under the same conditions, it is nevertheless true that as

each set of plants exists, under its own climate, the desert plant loses far more water in transpiration per unit area than does the plant of the rain-forest.

In the herbaceous plants of the rain-forest there is no correlation of stomatal openness and relative transpiration rate, at least during the morning and mid-day hours. These plants possess extremely thin epidermal structures, through which the loss of water in transpiration is found to be slightly greater than the loss through the stomata. The preponderance of cuticular transpiration is largely responsible for the fact that the total transpiration is extremely sensitive to the prevailing evaporation conditions and is partially responsible for the fact that the relative transpiration rate of these plants when placed in darkness is not lower than their rates in the light.

The writer's interest in the behavior of rain-forest plants has centered in the most hygrophilous forms, but these must not be taken as typifying the vegetation as a whole. The difference between the climate in the interior of the forest and in openings in the forest and the difference between the climate at the floor of the forest and in its canopy are as great as the normal difference between widely separated places. Corresponding with these differences of climate are striking differences in the character of the vegetation, both when the forest floor is contrasted with cleared thickets and when it is compared with the forest canopy. The dominant trees of the best developed rain-forest possess very sclerophyllous foliage; the high epiphytes have coriaceous succulent leaves; below them are to be found the normal leaves of the larger shrubs; beneath these the thin leaves of the larger herbaceous plants with an open mesophyll of several layers of cells; while in the lowest and most shaded situations are to be found such small plants as *Peperomia pellucida*, with a single layer of mesophyll cells, and the filmy ferns, with leaves which are a single layer of cells in thickness. This tremendous contrast between the members of the several layers of the rain-forest and the vertical differences of climate to which the contrast is chiefly due are both dependent upon the existence of the forest itself and the power which each stratum of vegetation has for the maintenance of the conditions which are vital to the plants of the next stratum below. The dominant trees and the high epiphytes are capable of withstanding the water loss to which they are subjected in the infrequent periods of cloudless weather, without fog or rain and with abnormally low humidity; while the hygrophilous plants of the lowest stratum are protected from the full duration of the dry periods by the shade in which they are growing and by the slowness with which the enormous quantities of moisture are given up by the soil, the rotting logs, the beds of mosses and hepatics, and the litter of fallen twigs and leaves.

There is no type of vegetation in which may be found a wider diversity of life forms than exist side by side or one above the other in a

tropical montane rain-forest. Together with the structural diversities, discoverable in the field or at the microscope, are diversities of physiological behavior, discoverable by observation or experiment, and sometimes correlated with the structural features. There are quite as high degrees of specialization to be found in the rain-forest as may be sought in the desert. The prolonged occurrence of rain, fog, and high humidity at relatively low temperatures places the vegetation of a montane rain-forest under conditions which are so unfavorable as to be comparable with the conditions of many extremely arid regions. The collective physiological activities of the rain-forest are continuous but slow; those of arid regions are rapid, but confined to very brief periods. In the regions of the earth which present intermediate conditions between those of the desert and the reeking montane rain-forest may be sought the optimum conditions for the operation of all essential plant processes. It is, indeed, in such intermediate regions—tropical lowlands and moist temperate regions—that the most luxuriant vegetation of the earth may be found, and it is also in such regions that the maximum origination of new plant structures and new species has taken place.

New York Botanical Garden Library
QK950.J2 S5
Shreve, Forrest/A montane rain-forest; a
gen
3 5185 00084 7663